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ORIGIN OF TUNDRA BUTTERFLIES IN ALBERTA, CANADA AND THEIR SIGNIFICANCE IN THE STUDY OF REFUGIA OF WISCONSIN AGE.

by

EDWARD M. PIKE

(C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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EDMONTON, ALBERTA

FALL, 1978

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled ..ORIGIN.OF.TUNDRA.BUTTERFLIES. IN.ALBERTA, CANADA AND THEIR SIGNIFICANCE IN THE STUDY OF ..... REFUGIA OF WISCONSIN AGE. .....

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Master of .....SCIENCE IN ENTOMOLOGY.

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Supervisor

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ABSTRACT

Four distribution types are recognized in the tundra butterfly fauna of Alberta: Type 1 (Southern Montane), Type 2 (Central Montane), Type 3 (Disjunct Populations), and Type 4 (Endemic forms). These indicate two source areas.

The major source area of tundra butterflies now found in Alberta was south of Wisconsin ice in the vicinity of northern Washington, Idaho, and Montana. Nine taxa survived in this unglaciated area, five showing a Southern Montane distribution, and four showing a Central Montane distribution. Taxa showing a Southern Montane distribution are Lycaena phleas arethusa, Lycaena snowi snowi, Oeneis polixenes brucei, Oeneis bore edwardsi, and Oeneis melissa beani. Central Montane distributions are shown by Colias nastes streckeri, Boloria astarte, Boloria alberta, and Euphydryas editha beani. This refugium was restricted to the east, west, and south by lack of suitable habitat for survival of these taxa. This indicates a narrow and discontinuous tundra belt south of Wisconsin ice. With retreat of Wisconsin ice, dispersal north was stopped by the elimination of continuous tundra in mountain valleys.

Taxa showing disjunct populations or endemic forms survived glaciations in an Albertan refugium in the vicinity of Mountain Park. The Albertan refugium did not contribute significantly to the colonization of present day Alberta tundra. Disjunct distribution was shown by Boloria improba youngi. Endemic forms were Boloria eunomia nichollae, Boloria napaea reiffi, and an ecological form of Oeneis melissa beani.

This investigation yielded detailed information on two isolated refugia. Therefore, the study of butterfly distribution patterns is deemed of great potential value in the study of Wisconsin glacial

refugia, in general.

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CHAPTER 1. INTRODUCTION

1. Introduction

Interest in the study and locations of Wisconsin Refugia has increased substantially in recent years, but rarely has an interdisciplinary approach been used in the investigation of a suspected refugium of Wisconsin age, one example being Karlstrom and Ball (1969). The logic behind this approach suggested that investigation of a previously unstudied segment of a supposed refugium biota was in order. Butterflies were chosen for a number of reasons. First, I was already familiar with the taxonomy of most North American butterflies. Second, butterflies form an important part of the tundra community. There are more species of butterflies on the arctic islands than there are of the order Coleoptera (Ryan, 1977). This indicates a high probability that they might survive the conditions of a tundra refugium. Thirdly, butterflies appear to differentiate more rapidly than many other insect taxa (Ford, 1946). The Rocky Mountains of Alberta were chosen as the study area because of the recent suggestion of a refugium in the Mountain Park area (Packer and Vitt, 1974), and because of the controversy over the extent of Wisconsin ice (Reeves, 1973).

Certain butterfly taxa have long been recognized as having relict distributions which reflect Pleistocene events (Grote, 1875; Maynard, 1886; Holland, 1898). Some biogeographical work has been done on these taxa (Klots, 1951, 1956; Ehrlich, 1956; Freeman, 1956) but none in much detail. In spite of the early recognition of these relict taxa, few subsequent workers have considered butterflies in studies of

suspected refugia in North America.

In numbers of species, butterflies form an important part of the tundra community. Based on an extensive literature search, one or more butterfly species occurs on every piece of tundra in North America where they have been investigated. A tundra refugium could therefore be expected to support at least some butterfly taxa. Investigation of the tundra butterflies of the Rocky Mountains of Alberta and their distributions would determine the value of butterfly distributions in studies of refugia, as well as elucidate indications of Wisconsin refugia in Alberta.

Information gained from these distributions, and from the comparison with distributions of other North American tundra butterflies, would indicate source areas of the Alberta fauna, as well as the presence of barriers to dispersal. Precise explanations can then be offered concerning the type and effectiveness of these barriers.

1.1 Thesis objectives

The objectives of this project were to determine the source areas for the tundra butterflies in Alberta, the probable route of immigration, and to elucidate the value of butterfly distributions in the study of refugia. I also identify barriers to dispersal, and offer explanations for the distributions shown by tundra butterflies in Alberta.

1.2 Tundra butterflies species

A tundra butterfly species is defined as a taxon in which reproduction is confined to areas above treeline. this definition includes both arctic and alpine taxa. Arctic and alpine environments intergrade extensively, as do the butterfly faunas. The existence of

tundra is usually defined through reference to treeline. Treeline is used in this study to delineate the lower, or southern, boundary of the subarctic and subalpine zone as defined by Löve (1970). This is line of economicly important timber (subarctic), or the line of continuous forest (subalpine). This is neccessitated by the occurrence of tundra butterflies south of the actual limit of trees.

Many individuals of some non-tundra butterfly taxa breed above treeline. Adults of these species are able to disperse below treeline. If these species survived in a refugium, post-glacial dispersal of adults and the resulting gene flow might obscure any indications of this survival resulting from isolation in the refugium. For this reason, these taxa are excluded from the study.

Because of limited dispersal abilities of most species used as indicators of refugia, and the island nature of alpine tundra, taxa restricted to tundra conditions provide the best biological evidence for identifying sites of Wisconsin alpine refugia.

1.3 Use of the term refugium

A number of terrestrial refugial types have been recognized (Lindroth, in Karlstrom and Ball, 1969). These are: Nunataks (exposed mountain tops extending above the level of continental ice); Coastal refugia (low altitude areas around edges of continental ice sheets on coast lines); and Continental refugia (large unglaciated areas, eg. North America south of Wisconsin ice, Beringia). While the last type is most important in terms of evolution and dispersal, virtually all discussion and controversy centers on the first two types. For the remainder of this thesis the word refugium applies only to these types,

and to a fourth type possible in Alberta: low altitude expanses of unglaciated area similar to coastal refugia, but not along a coast line. This will be explained further, later in the text.

CHAPTER 2. MATERIALS AND METHODS

This section will cover the number of specimens examined, their deposition, and sources of data and identifications. The use of the trinomial is discussed, and assumptions basic to the interpretation of the data are explained.

2.1 Materials

2.1.1 Specimens examined

During the course of this study, 868 specimens of tundra butterflies were collected in Alberta and British Columbia. Of these, 723 represent taxa found in Alberta. A further 720 specimens were examined from the collections of E. M. Pike, F. Sperling, T. Thormin, G. Hilchie, and the University of Alberta Strickland Museum. A total of 1588 specimens were examined.

2.1.2 Deposition of material

Specimens collected within the boundaries of Jasper and Banff National Parks are deposited in the Canadian National Collection, Ottawa, Ontario; University of Alberta Strickland Museum, Edmonton, Alberta; Jasper and Banff Parks Headquarters. Remaining specimens are deposited as follows; voucher specimens to the University of Alberta Strickland Museum, selected series to my collection, and some material was exchanged for specimens for further research.

2.1.3 Sources of records

Sources of records are as follows: ROCKY MOUNTAINS SOUTH OF 49°N; preliminary maps for a book on the butterflies of the southern Rocky Mountains (Stanford, 1977). ALBERTA: C. D. Bird, Calgary; personal collections

BRITISH COLUMBIA: J. Shepard, Nelson, British Columbia; personal collections; NORTHERN TUNDRA: Freeman (1956), Lepidopterists' Society Season Summaries (1973-1976), Alaska Lepidoptera Survey Summary (Philips, 1970), revisions of Oeneis taygete and Erebia youngi (dos Passos, 1947, 1949), personal collections.

2.2 Methods

2.2.1 Determination of taxa

Identifications to species level are based primarily on Ehrlich and Ehrlich (1961). Subspecific identifications were based on original descriptions, revisions and discussions from the literature, and published descriptions of ranges. Where adequate descriptions of ranges were not available, identifications were made according to the proximity of collecting sites to subspecific type localities, and by probable ecological similarity of these sites to the type localities.

2.2.2 Use of the trinomial

Because this project is not a revision, subspecies are accepted as presented in dos Passos (1964), as modified by more recently published information. None of these subspecies have been adequately investigated, and many may be ecomorphs. Application of the subspecies concept has been highly variable in the past and it is still not uniform. Most distinctive populations in North America have been formally named. Even though many of these names may not be valid taxonomically, they do provide convenient sources of reference to recognizably distinct populations. This is the sole reason for their use in this study. All subspecies of tundra butterflies in Alberta are fairly distinct, and are readily placed with populations outside the province. This allows

reasonably secure hypotheses about their evolution and dispersal into Alberta.

2.2.3 Synthesis of data

Locality data were organized by species. These are presented in appendix 1. Localities were plotted with the aid of the following: ALBERTA - Atlas of Alberta (1969), Gazetteer of Alberta (1974); BRITISH COLUMBIA - Gazetteer of British Columbia (1966), British Columbia relief map (1968); NEWFOUNDLAND AND LABRADOR - Gazetteer of Newfoundland and Labrador (1968), Times World Atlas (1957); NORTH WEST TERRITORIES - Gazetteer of the North West Territories (1971), Times World Atlas (1957); QUÉBEC -Gazetteer of Québec (1969), Times World Atlas (1957); YUKON TERRITORY - Gazetteer of the Yukon Territory (1976), Times World Atlas (1957); ALASKA -Dictionary of Alaska Place Names (Orth, 1976), United States Department of the Interior, Geological Survey Map B, Alaska (1955). Because Gazetteers were not available for Washington and Montana (United States), topographic maps were examined in an attempt to accurately locate collecting sites.

The topographic map of the eastern slopes of the Rocky Mountains in Alberta was modified from pages 10 and 11 of the Atlas of Alberta (1969). Figure 1 shows the relationship between this area and the rest of Alberta.

2.2.4 Zoogeographic assumptions

Zoogeography is the scientific study of the distribution of animals on earth (Udvardy, 1969). The distribution of a given taxon in the result of two factors. The first is the history of past events

to which a taxon has been exposed. The second is the response of the taxon to these events. In order to attempt to explain the distribution of any taxon, we must first understand the sequence of geologic, climatic, and ecologic events which might have affected it. A major assumption, then, is that our knowledge of these events is fairly complete and accurate.

A second major assumption is that our knowledge of a taxon's distribution is accurate. If this knowledge is not accurate, further discoveries may place conclusions based on this faulty knowledge in jeopardy. It is safe to assume that knowledge of the ranges of most tundra butterflies is accurate, because of intensive collecting during the past ten years. Taxonomy at the species level is generally sound. Specific problems are discussed in the species synopsis.

Given these assumptions, we can then proceed to examine the data. Hypotheses and conclusions should be presented in a manner such that they are open to falsification, and in sufficient detail to allow future testing (Ball, 1975).

2.2.5 Taxonomic errors

If a specimen is identified incorrectly, the known distributions of the species to which it actually belongs, and the species with which it is identified, are affected. This has caused considerable confusion in the past. It is still an important factor in arctic areas and at boundaries between subspecies.

2.2.6 Collecting bias

The following factors influence our perception of the distributions of taxa. Their bearing on the second assumption mentioned above is discussed.

2.2.6.1 Geographical bias

Certain areas of the province have been collected more extensively or intensively than others. Large areas remain virtually unexplored in terms of tundra butterflies. This is due largely to accessibility and location of collectors. The only area where this factor might affect our interpretation of the ranges of tundra butterflies in Alberta is in the region north west of Hinton. This is discussed under the section dealing with source areas of Alberta tundra butterflies.

2.2.6.2 Temporal bias

In Alberta, the mountains are not usually visited by collectors until middle or late July. Species whose adults fly in June or August may be missed.

2.2.6.3 Personal bias

When a collector is in the field, he or she is inclined to concentrate on areas where specimens are numerous, or where the terrain is easiest to traverse. Species confined to other areas are likely to be missed. A collector may also be limited by physical ability.

2.2.7 Factors influencing distributions

Ranges of taxa are limited by the nature of each (its hyperspace, or niche), and by the history and nature of the physical environment. Specific factors which affect the distributions of tundra butterflies in Alberta are mentioned below.

2.2.7.1 Hyperspace

Each taxon has a distinctive assemblage of ecological requirements. These determine the total habitat available. Each taxon survives only where at least the minimum resource requirements are met.

2.2.7.2 Physical relief

Altitude, topographical and geological features of the ground surface are included here. These, in part, determine where the ecological requirements of each species will be met.

2.2.7.3 Continental glaciations

This is the first of two climatic factors. It includes the presence and effects of continental ice sheets. The last major glaciation in Alberta was of Wisconsin age, and previous workers believed it to have caused the extinction of terrestrial life in all but the southern-most parts of the province (Flint, 1957; Prest, 1969). Recent work does not support this hypothesis, but in either instance, the effects of this glaciation on the tundra butterfly fauna would have been substantial.

2.2.7.4 Post-glacial events

The Post-glacial period began with the melting and breakup of Wisconsin continental ice sheets in North America. It represents the period of time available for colonization and redevelopment of plant and animal communities in areas recently vacated by ice.

2.2.7.5 Colonization ability

The ability of a taxon to colonize an available habitat depends on four factors:

a) distance to available habitat, including physical distance as well as the presence or absence of barriers;

b) dispersal capabilities of the taxon;

c) time since the habitat became available;

d) interspecific competition.

Ecological requirements determine suitable areas where taxon can exist. Post-glacial events and colonization ability affect the taxon's ability to reach these areas. These factors combine to give the actual distribution.

Recognizing the limitations in our present knowledge of the tundra butterfly fauna in North America, we can examine the distributions shown by this fauna in hope of assessing the effects of the last glaciation on this fauna, and determine the source areas of this fauna as represented in Alberta.

2.2.8 Identification of refugia

The presence of a refugium in a given area is inferred from a number of kinds of evidence.

2.2.8.1 Geological evidence

A mobile ice sheet leaves certain geological indications of its existance. Absence of indications of ice movement is usually taken as indication that ice was not present. Permanent snow fields and sessile ice masses cannot be detected.

Unfortunately, geological data are not often available to the biologist because of lack of investigation, or because crucial data that are available are interpreted differently by different geologists.

2.2.8.2 Endemic taxa

The best biological evidence of a refugium is the presence of a number of endemic taxa in an area that was previously considered covered by ice.

Presence of endemic taxa implies isolation over a fairly long period of time, or at least sufficient time for divergence to occur.

Isolation implies terrain on which to survive and reproduce, or a refugium.

2.2.8.3 Disjunct populations

The most common biological indicator of a refugium is presence of disjunct populations of a number of taxa concentrated in the same area. Disjunct populations are interpreted as having survived in an ice free area while considerable portions of the former range of the species were eliminated by overriding ice. In order for this interpretation to be valid, various other explanation must be eliminated: long range dispersal, relict populations due to other factors (Wynne-Edwards, 1937; Morisset, 1971), and collecting bias.

2.2.8.4 Genetic polymorphism

The last type of biological evidence is genetic polymorphism. Lindroth (1949) has used distribution of brachypterous carabid beetles as evidence of refugia in Scandinavia. The brachypterous populations result from genetic depletion through dispersal of winged forms during the glacial maxima. Coope (1969) offers an alternate explanation of their presence in Scandinavia. He suggests that they arrived there via ice rafting, but still considers the brachypterous form to have developed in a refugium; English rather than Scandinavian. Thus it remains that this kind of information is a potentially valuable indicator of refugia.

The strongest argument for the presence of a refugium will contain examples and evidence from all of the four types mentioned above.

CHAPTER 3. STUDY AREA

The area under study includes all known tundra which has been examined for butterflies in North America, but the focus of attention is on tundra in Alberta. Tundra areas extend from the Sierra Nevada of California and the Sangre de Cristo range of New Mexico (approximately 36° north latitude) at elevations of over 3384 meters (11,000 ft.), north to the limit of land on Ellesmere Island and Greenland (approximately 83° north latitude). In eastern North America, isolated areas of tundra occur as far south as Mount Marcy, New York, and Mount Washington, New Hampshire (approximately 44° north latitude) and elevations of just over 1358 meters (5000 ft.).

In Alberta, tundra extends from the United States border (49° N.) north to about 54° 20' N, where the Rocky Mountains leave the province. Occurrence of tundra roughly parallels the Alberta-British Columbia border along the continental divide. It is usually above 1970 meters (6500 ft.) in the northern areas of the province, gradually increasing in elevation to the point where it is not found below 2153 meters (7000 ft.) at 49° N.

3.1 Formation of the Rocky Mountains

Most of the Rocky Mountains took their present form during two major orogenic periods: the Sevier and Laramide revolutions. The Sevier ranged in time from about 140 to 60 million years ago and forms the western ranges of California, Oregon, Washington, and British Columbia (Grose, 1972; Clark and Stearn, 1960). The Laramide orogeny lasted from 70 to 55 million years ago and formed all of the eastern mountain

systems from British Columbia and Alberta south to New Mexico (McGookey et. al., 1972; Clark and Stearn, 1960). Volcanic and minor tectonic activity have continued into historical times. In Alberta, the Rocky Mountains consist almost entirely of limestones of Precambrian, Cambrian, Devonian and Mississippian age (Clark and Stearn, 1960).

3.2 Flora

While environmental parameters vary greatly between different areas of tundra, the tundra plant community is similar, being of low relief with a high percentage of perennial herbs and shrubs (Kershaw, 1973). Except for scattered krumholtz usually less than two meters high, trees are absent.

In Alberta, tundra in the Crowsnest pass area and Waterton National Park is considerably different from tundra to the north (Kuchar, 1975). In Waterton, there are more endemic species (Packer, 1971), and Dryas and heath communities are less prominent (Kuchar, 1975).

Characteristic plant genera include Carex, Poa, Salix, Dryas, Saxifraga, Draba, and Oxyria. Lichens form a large proportion of the species present compared to tundra farther south (Kuchar, 1975).

3.3 Fauna

In Alberta, vertebrates that frequent the tundra environment include Ptarmigan (Lagopus), Hoary Marmots (Marmota marmota), Columbian Ground Squirrel (Spermophilus columbianus), Mountain Goat (Oreamnos americanus), Big Horn Sheep (Ovis canadensis), and Pika (Ochotona princeps). None of these are restricted to tundra, and most have a

western montane distribution.

Invertebrates that occur on tundra are too numerous to mention, but it is important to note that many groups of invertebrates have developed species and genera which are entirely restricted to tundra conditions.

3.4 Development of tundra biotas

3.4.1 Flora

Most of the genera of plants were derived from lower elevation during the Tertiary, and are not restricted to tundra (Löve and Löve, 1974). This is true of many of the species as well (Chabot and Billings, 1972). While alpine floras may have been present since the Tertiary (Packer, 1974), arctic floras do not appear to have evolved before the late Pliocene (Savile, 1972).

Tundra flora in Alberta north of Waterton National Park is more similar to upland arctic tundra than to tundra in the Rocky Mountains south of the Canadian border (Kuchar, 1975; Hrapko, 1970). This is contradictory to relationships of Alberta tundra butterflies, which are discussed in section 6.3.

3.4.2 Fauna

There are no vertebrates restricted to tundra in Alberta, but there are a few in the arctic, one example being the Musk Ox (Ovibos moschatus). As mentioned earlier, there are a considerable number of invertebrates restricted to tundra. Macpherson (1965) discusses the historical development of arctic tundra mammals in Canada.

3.4.3 Trends

The tundra biota, on the whole, is a depauperate one compared to other communities. This has been well documented with respect to vascular plants (see Kuchar, 1975 for discussion), and is also true for mammals (Macpherson, 1965). The butterfly community is also somewhat reduced compared to most other areas in the province.

CHAPTER 4. WISCONSIN AND POST-GLACIAL EVENTS

4.1 Extent of Wisconsin ice in Alberta

To understand the effect this glaciation had on the flora and fauna in Alberta, we must first discuss its probable extent. It is also necessary to point out conflicts in interpretation of the sedimentary record which might affect the outcome of this study.

4.1.1 Western limit of Laurentide ice

From Calgary, north to Hinton, the western limit of Laurentide ice is well established (Roed, Mountjoy and Rutter, 1967; Boydell, 1968; Curry, 1976; Reimchen and Bayrock, 1977; Stalker, 1977). This limit is generally agreed to represent Classical Wisconsin ice. Early Wisconsin ice is generally thought to have been more extensive, reaching farther west (Reimchen and Bayrock, 1977; Alley, 1973).

There is a difference of opinion about the limit of Laurentide ice during the Classical Wisconsin, south of Calgary. One group of authors maintains that the ice limit of Classical Wisconsin age was west of Calgary extending south to well west of Lethbridge (Jackson, 1977; Alley, 1973). Another group of authors suggests that Classical Wisconsin ice advances terminated east of Calgary and just west of Lethbridge (Reeves, 1973; Stalker, 1977). Early Wisconsin ice is considered to have been more extensive (Reimchen and Bayrock, 1977; Stalker, 1977; Alley, 1973; Reeves, 1973).

4.1.2 Eastern limit of Cordilleran ice

The eastern limit of Cordilleran ice has been the subject of less controversy than the limits of Laurentide ice in Alberta. Reeves (1973) maintains that ice on the eastern slope of the Rocky Mountains

consisted of isolated valley and piedmont glaciers which continued to be independent of each other throughout the Wisconsin. More recent work has indicated that the Cordilleran ice sheet was considerably more extensive in the northern areas from Hinton south to about High River (Roed, Mountjoy and Rutter, 1967; Rutter, 1971; Boydell, 1968; Jackson, 1977; Reimchen and Bayrock, 1977) forming an extensive ice sheet in the Early Wisconsin, and a smaller, but still fairly cohesive, sheet in Classical Wisconsin times. Cordilleran ice was very limited from the Chain Lakes south to Waterton National Park. The hypothesis of complete glaciation advocated by some (Flint, 1957; Prest, 1969) is not supported by recent work cited above.

4.1.3 Extent and age of coalescence

Investigations of surficial geology have yielded data that indicate Laurentide and Cordilleran ice coalesced extensively (Jackson, 1977; Boydell, 1968; Boydell, Bayrock and Reimchen, 1974; Roed, Mounjoy and Rutter, 1967). These are generally assumed to be either Early or Classical Wisconsin by the authors. Unfortunately, radiocarbon dating and stratigraphic controls are largely lacking from Alberta (Reeves, 1973; Stalker, 1977). This makes correlation of sequences hazardous, and is a major problem in reconstructing Wisconsin events in Alberta. The most recent attempt at correlation of Cordilleran tills is shown in Figure 2. Using this as a basis for discussion, it appears that Cordilleran ice advances were essentially synchronous. Figures 2, 3 and 4 suggest that in Early Wisconsin times, Laurentide and Cordilleran ice were essentially continuous, and that in Classical Wisconsin times, coalescance as sporadic, but extensive. Various ice frontal positions are shown in Figures 3 and 4.

4.1.4 Unglaciated areas

From Figures 3 and 4, it can be seen that large areas in the mountains and foothills were unglaciated in both the Classical and Early Wisconsin. These areas are generally over 2461 meters (8000 ft.) in the mountains proper, but in the foothills and particularly in the Crowsnest Pass area, they extend down to about 1230 meters (4000 ft.). Much of this unglaciated terrain would have been uninhabitable exposed bedrock, or above the limit of plant growth, but there would have been considerable area available for survival of tundra. Geological data indicated a good possibility of biological refugia in Alberta during the Wisconsin.

4.2 Post-glacial events

The Post-glacial episode has not been adequately investigated in Alberta. The only works have been a soil profile study in the Cypress Hills area (Jungerius, 1969) and some pollen core work by Hansen, and Lichti-Federovich (1970). Most of the geological works mentioned above indicate two or three Post-glacial advances in glaciers, all minor. These have not been dated, but the youngest one is of historical age. A "little ice age" has been documented in many areas, and is probably equivalent to the oldest Post-glacial advance in Alberta.

Also documented in other areas is a period of time when the climate was warmer than present, during which treeline advanced to a position much farther north than at present (Bryson, et. al., 1965; Nichols, 1967). Maher (1961) indicates that at one time treeline in

Colorado was 200 m. (600 ft.) above the present treeline. It is reasonable to expect that treeline in Alberta would react in a similar way, but to a lesser extent. If it were raised 75 m. (240 ft.), many lower elevation tundras would have been eliminated. With a later lowering of treeline, these would redevelop and become available for colonization. A likely example would be Coliseum and Shunda mountains near Nordegg (see Figure 5). These extend about 6 and 50 m. (20 and 160 ft.) above treeline respectively. Any major rise in treeline would have extinguished tundra communities on these peaks. With the end of the hypsithermal, treeline probably retreated downward giving tundra a chance to re-establish, both from sheltered areas on the mountain tops, and by dispersal from nearby mountains.

CHAPTER 5. SPECIES SYNOPSIS

Where possible, sequence and classification follow dos Passos (1964). Numbers following names refer to this ordering. Changes reflect recent descriptions or instances where status of taxa have been questioned. Asterisks preceding a name indicates that the taxon has been recorded from Alberta.

5.1 Parnassius eversmanni thor H. Edwards, 1881 #243

Type locality; upper reaches of the Yukon River.

Geographical Distribution

Known distribution is given in Figure 6. This species is also recorded from arctic Europe and Asia, southward on numerous mountain ranges, with one disjunct population in Japan. In North America, this subspecies has dispersed outside of Beringia only to adjacent mountain ranges in British Columbia, where it is represented by two populations whose ranges are disjunct from one another.

Material examined: 79 specimens.

5.2 Colias boothi Curtis, 1835 #285

Type Locality: Boothia peninsula, North West Territories.

Notes

Adults of this species have been confused by taxonomists in the past with those of C. nastes and C. hecla, and the species was once thought to represent a hybrid of these taxa. It is now

recognized as a distinct species, but some taxonomists still confuse specimens with those of yellow populations of C. nastes, particularly C. n. thula (Philip, in The Lepidopterists' Society season Summaries, 1974, 1975, 1976). Populations of C. n. thula are sympatric with those of C. n. aliaska. This indicates three possibilities: C. n. thula is a species distinct from both C. boothi and C. nastes; C. n. thula is an Alaskan subspecies of C. boothi; C. n. thula is a "form" of C. nastes not deserving taxonomic recognition. Because neither C. n. thula or C. boothi are found in Alberta, this problem does not affect the outcome of this project.

Geographical Distribution

Distribution is indicated in Figure 7, along with that of C. n. thula which is plotted here to show that the two are allopatric. C. n. thula is restricted to northern Alaska, C. boothi to the North West Territories and the Yukon Territory.

Material examined: 2 specimens.

5.3 Colias nastes Boisduval, 1832 #296

Seven subspecies are currently recognized.

C. n. nastes Boisduval, 1932

Type Locality: Labrador (Ungava Peninsula).

C. n. rossi Guenee, 1864

Type Locality: Boothia Peninsula, North West Territories.

C. n. moina Strecker, 1880

Type Locality: Churchill, Manitoba.

* C. n. streckeri Grum-Grschimailo, 1895

Type Locality: Laggan, Alberta (Lake Louise).

C. n. cocandicides Verity, 1911

Type Locality: unavailable.

C. n. thula Hovanitz, 1955

Type Locality: Meade River, Alaska.

C. n. aliaska Bang-Haas, 1927

Type Locality: unavailable

Notes

C. n. streckeri includes only green colormorphs, which exhibit slight, but constant variation. Adults were first collected on a number of mountains in the vicinity of Laggan, Alberta, by T. E. Bean. It has since been reported from many mountains in Alberta. Colonies probably exist in the province wherever tundra has developed. Specimens are usually abundant, although often difficult to catch. Populations from Pink Mountain, British Columbia, are provisionally assigned to this subspecies.

This species has not been adequately treated in a revision. If it were, it is probable that some of the presently accepted names would be synonymized.

Geographical Distribution

Distribution is shown in Figures 7 and 8. This species is also known from Europe and Asia. In North America, it is recorded from Alaska, Yukon and North West Territories, Quebec, Manitoba, Labrador, British Columbia, and Alberta, Washington, and Montana. Alberta distribution is indicated in Figure 29.

Exact limits of the subspecies are not known in the arctic, although the range shown on the map is probably close to the actual range of the species.

Material examined: 264 specimens.

5.4 Lycaena phleas (Linnaeus, 1761) #443

Four subspecies are recognized, only three of which are restricted to tundra habitat.

L. p. hypophleas (Boisduval, 1852)

Type Locality: Sierra of California.

* L. p. arethusa (Wolley-dod, 1907)

Type Locality: Sheep River, 30 miles south west of Calgary, Alberta.

L. p. feildeni (M'Lachlan, 1878)

Type Locality: Ellesmere Island, 81° 41' N., North West Territories.

Notes

The distribution patterns and relationships between the various subspecies in Europe and North America are poorly understood. In North America, one subspecies, L. p. americana, does not occur on tundra. Also, while L. p. arethusa specimens are encountered most often above treeline, some range well below treeline in Alberta. The type locality, if taken literally, is well below treeline, although Wolley-dod may have been referring to the headwaters of the Sheep River, which are much higher in elevation. At, and north of, Mountain Park,

specimens have been taken below treeline more regularly; at Mountain Park, Prospect Mountain, Moberly Creek, and Grande Cache. In spite of intensive collecting in recent years, specimens have not been found below treeline south of Mountain Park. For this reason, boreo-montane populations are here considered to be derived from alpine populations, and this subspecies is considered a tundra butterfly. It is also possible that the low altitude populations represent a distinct taxon separate from the alpine populations.

Geographical Distribution

L. p. arethusa is found as far south as Colorado, and as far north as Grande Cache, Alberta. The nominotypical form is European. This species is found over much of Europe and Asia. The Nearctic distribution is indicated in Figure 9. Alberta distribution is indicated in Figure 30.

Material examined: 33 specimens.

5.5 Lycaena snowi (Edwards, 1881) #445

Two subspecies are recognized.

* L. s. snowi (Edwards, 1881)

Type Locality: Colorado.

L. s. henryae (Cadbury, 1937)

Type Locality: Cariboo Pass, Peace River Country, British Columbia.

Notes

L. s. henryae has not been collected since its description. L. s. snowi was first collected in Alberta by T. E. Bean in the

vicinity of Laggan. However, specimens are more commonly encountered to the south than to the north in the province. In Alberta, it appears to be restricted to above treeline, but in Wyoming, it has been reported below treeline (Howe, 1975; Ferris, 1971).

Opinions differ about the relationship of this species to L. cupreus, whose range is below treeline in California, north east to Colorado. Howe (1975) and Ehrlich and Ehrlich (1961) consider the two groups conspecific. Dos Passos and most previous authors consider them distinct. I follow dos Passos. Certainly the two taxa are closely related. However, this taxonomic problem does not affect the outcome of this project because the Alberta material is clearly similar to L. snowi of Colorado.

Geographical Distribution

Distribution is indicated in Figure 10. L. snowi is found from Colorado north to central British Columbia. It has not been reported from the Yukon Territory or Alaska. Alberta distribution is indicated in Figure 31.

Material examined: 21 specimens.

5.6 Euphydryas editha (Boisduval, 1852) #595

Eighteen subspecies are currently recognized. Of these, only four are restricted to tundra. These are treated below.

E. e. nubigena Behr, 1863

Type Locality: Headwaters of the Tuolumne River and beyond to elevations of 11500 ft. (3538 m.), California.

E. e. lawrenci Gunder, 1931

Type Locality: Mount Theilsen, Douglas County, Oregon.

E. e. colonia Write, 1905

Type Locality: Mt. Hood, Oregon.

* E. e. beani Skinner, 1897

Type Locality: High elevations near Laggan, Alberta (Lake Louise).

Notes

While most subspecies of E. editha are not found on tundra, these four subspecies appear to be restricted to tundra environments, which they evidently colonized recently, apparently in response to empty niches on the mountains they inhabit. With the exception of E. e. beani, they occur where there are virtually no other tundra butterflies.

E. e. beani has been reported more commonly to the south of the type locality, where specimens were collected by T. E. Bean. Specimens are easily confused with alpine specimens of E. anicia. The northern records of E. e. beani are older, and may represent misidentifications, but most of the southern records have been verified in recent years.

Geographical Distribution

Distributions are indicated in Figure 11. E. e. beani is restricted to the mountains of southern Alberta and British Columbia and E. e. nubigena is restricted to the high Sierra of California. The other two subspecies have only been recorded from their type localities. Alberta distribution is indicated in Figure 32.

Material examined: 27 specimens.

5.7 Boloria napaea (Hoffmansegg, 1804) #597

The nominotypical form is European. Four subspecies have been recorded from North America.

B. n. alaskensis (Holland, 1900)

Type Locality: Mountains between 40 mile and Mission Creeks, Alaska.

B. n. nearctica Verity, 1932

Type Locality: North eastern Alaska.

* B. n. reiffi Reuss, 1925

Type Locality: Mountains of British Columbia.

B. n. halli Klots, 1940

Type Locality: Green River Pass, Wind River Mountains, Wyoming.

Notes

Shepard (in Howe, 1975) has made B. n. reiffi a junior synonym of B. n. alaskensis. This is without warrant, for it is not based on study of the type specimen, but rather on conjecture by Klots (1940) and Warren (1944). Specimens of B. n. reiffi have been recorded from Kvass Creek Summit and the headwaters of the Berland River, Alberta. I adopt this assignment because of the proximity of the type locality.

In the past, these subspecies were treated under the name B. pales (Denis and Schiffermuller, 1775). Warren (1944) placed them under the name B. napaea. This is generally accepted, but it is based on characters of doubtful significance.

Geographical Distribution

Distribution is indicated in Figure 12. This species is common in arctic and alpine areas of Europe and Asia. In North America, it is found in Alaska, Yukon Territory, and arctic North West Territories excluding the northern-most arctic islands. It has been reported in northern British Columbia, and as disjunct populations in central Alberta, and in Wyoming. Alberta distribution is indicated in Figure 33.

Material examined: 69 specimens.

5.8 Boloria improba (Butler, 1877) #601

Two subspecies are recognized.

B. i. improba (Butler, 1877)

Type Locality: Winter Cove, Cambridge Bay, North West Territories.

B. i. youngi (Holland, 1900)

Type Locality: Mountains between 40 mile and Mission Creeks, Alaska.

Notes

B. improba was first reported from Alberta in 1976 from Prospect Mountain (see Figure 5). Eleven specimens have been collected. Adults of this population appear most similar to those of B. i. youngi, and the Alberta population is so placed, but it may deserve subspecific status. Adults show constant and remarkably stable differences from adults of other examined populations. This is a highly variable species year to year, so longer series are needed

before a decision can be made.

Geographical Distribution

Distributions of the two subspecies are indicated in Figure 13. This species is also known from arctic Europe and Asia. In North America, it is found in Alaska, the Yukon Territory, arctic North West Territories excluding the high arctic islands, northern British Columbia, and a disjunct population in west-central Alberta. Alberta distribution is indicated in Figure 34.

Material examined: 89 specimens.

5.9 Boloria polaris (Boisduval, 1829) #604

Three subspecies are recognized.

B. p. polaris (Boisduval, 1829)

Type Locality: Norwegian Alps.

B. p. groenlandica (Skinner, 1892)

Type Locality: Greenland.

B. p. stellata Masters, 1972

Type Locality: Churchill, Manitoba.

Notes

Adults of this species are rarely collected, although they are often abundant. Unlike most butterfly species, very few infraspecific names have been proposed for this taxon.

Geographical Distribution

This species is found from Lappland across arctic Europe and Asia to Greenland. In North America, it is recorded from Alaska, Yukon Territory, North West Territories including the high arctic islands,

Manitoba, Quebec, Labrador, and northern British Columbia. Distribution is indicated in Figure 14.

Material examined: 166 specimens.

5.10 * Boloria alberta (Edwards, 1890) #606

Type Locality: Laggan, Alberta (Lake Louise).

Notes

This species has been reported from Anaktuvuk Pass, Alaska, but because worn adults of B. polaris and B. distincta resemble those of B. alberta, this record must be regarded as suspect.

Geographical Distribution

This species is restricted to high alpine areas in northern Montana, and southern Alberta and British Columbia. A different subspecies has been reported from the U.S.S.R. Nearctic distribution is indicated in Figure 15. Alberta distribution is indicated in Figure 35.

Material examined: 43 specimens.

5.11 *Boloria astarte (Doubleday, 1846-1852(1847)) #607

Type Locality: Mountains of British Columbia, here restricted to Mt. Cheam.

Notes

Dos Passos (1964) and Shepard (in Howe, 1975) recognize two subspecies; B. a. astarte and B. a. distincta. Wyatt (1957) discounts the hypothesis that they are conspecific. Because of numerous differences between the two taxa, I follow Wyatt. Certainly they are easily separated, but closely related. The problem does not affect

the outcome of this project.

Type locality is the mountains of British Columbia. Edwards (1891) proposed the name Argynnis victoria which he later recognized as a junior synonym of B. astarte. The type locality for A. victoria is Laggan, Alberta (Lake Louise).

At the time of the description of B. astarte, British Columbia's boundaries were poorly defined or non-existent, and the area around Laggan was unexplored. It seems reasonable to restrict the type locality of B. astarte to the locality nearest the major cities of British Columbia around 1800-1820. The type locality is hereby restricted to Mount Cheam, south of Hope, British Columbia, where lives the population closest to Vancouver Island and the mouth of the Frazer River.

Geographical Distribution

Distribution is indicated in Figure 16. This species is recorded from British Columbia, Alberta, and northern Washington and Montana. Alberta distribution is indicated in Figure 36.

Material examined: 59 specimens.

5.12 Boloria distincta (Gibson, 1920) #607b

Type Locality: Harrington Creek, Yukon Territory.

Geographical Distribution

In North America this species appears to be restricted to Beringia with one record from Atlin, British Columbia and a few from the Richardson Mountains, North West Territories. Distribution is

indicate[illegible]ure 17.

Material examined: 15 specimens.

5.13 Boloria eunomia (Esper, 1787) #610

Seven subspecies are recognized in North America, four of which are restricted to tundra (includes alpine bogs) conditions above treeline.

B. e. caelestis (Hemming, 1933)

Type Locality: Hall Valley, Park County, Colorado.

B. e. ursadentis Ferris and Groothuis, 1971

Type Locality: Beartooth Plateau, Wyoming.

* B. e. nichollae (Barnes and Benjamin, 1926)

Type Locality: Rocky Mountains of North America, here restricted to the north end of Wilcox Pass, Columbia ice fields, Jasper National Park, Alberta.

B. e. laddi (Klots, 1940)

Type Locality: Lewis Lake, Albany County, Wyoming.

Notes

B. e. nichollae was misidentified by Shepard (in Howe, 1975). His identification was based on the fact that according to the published itinerary of the original collector's trip west (Nicholls, 1905), she did not and could not have collected in the area where a dark form corresponding to the description is found. However, she made a later trip west, as indicated by records of B. alberta and B. astarte collected by her at the headwaters of the Saskatchewan and Athabasca Rivers, Alberta (Entomological Society of Ontario,

records; seasonal collection list, 1907). This area is the center of the distribution of the dark form of B. eunomia. This suggests that Mrs. Nicholls could have collected the type series during her second trip. This is supported by a paratype from the USNM which is darker than normal adults from most areas in the mountains of Alberta. Accordingly, the type locality is restricted to the north end of Wilcox pass, Columbia Ice Fields, Jasper National Park, Alberta. This pass was chosen because before the highway was built between Jasper and Lake Louise, the only way to cross from the Athabasca watershed to that of the Saskatchewan River was via this pass by pack train (J. Pike, personal communication). If Mrs. Nicholls collected in both watersheds, she must have used this pass, and probably collected there as evidenced by the type series of B. e. nichollae.

Geographical Distribution

Distributions of the four subspecies are indicated in Figure 18. B. e. nichollae is restricted to west-central Alberta, B. e. ursadentis to its type locality (Beartooth Plateau, Wyoming), B. e. laddi to Wyoming, and B. e. caelestis to Colorado. There has been one record of B. e. laddi from Colorado, but this has been questioned. Alberta distribution is indicated in Figure 37.

Material examined: 184 specimens.

5.14 Oenis bore (Schneider, 1792) #667

Included here is O. taygete Geyer, 1830. Six subspecies are recognized.

O. b. taygete Geyer, 1830

Type Locality: Hopedale, Labrador.

O. b. gaspeensis dos Passos, 1949

Type Locality: Mount Albert, Quebec.

O. b. fordi dos Passos, 1949

Type Locality: Kuskoquim River Valley, Alaska.

* O. b. edwardsi dos Passos, 1949

Type Locality: San Juan Mountains, Hinsdale County, Colorado.

O. b. hanburyi Watkins, 1928

Type Locality: Coronation Gulf, North West Territories.

O. b. mackinleyensis dos Passos, 1949

Type Locality: Mount Mckinley National Park, Alaska.

Notes

Adults of these subspecies are very similar to one another. Alberta material was ascribed to O. b. edwardsi by dos Passos in his description. Adults were first collected in the province at Nordegg by K. Bowman.

Adults of what is usually considered O. taygete are distinguished by the presence of white outlined veins on the ventral hind wings. This character does not appear to be constant, so these subspecies are placed under the name O. bore. Either way, the outcome of this project is not affected.

Geographical Distribution

Distribution is indicated in Figure 19. This species is found in Alaska, Yukon Territory, arctic North West Territories excluding the high arctic islands, Quebec, Manitoba, Labrador, northern British

Columbia, Alberta, Montana, Wyoming, and Colorado. There is one record from Utah. It is also known from Europe and Asia, along the coast of the Arctic Ocean. Alberta distribution is indicated in Figure 38.

Material examined: 156 specimens.

5.15 Oeneis melissa (Fabricius, 1775) #670

Seven subspecies are recognized.

O. m. melissa (Fabricius, 1775)

Type Locality: Newfoundland.

O. m. semplei Holland, 1931

Type Locality: Little Cape James River; Churchill, Manitoba; Hudson Bay.

O. m. assimilis Butler, 1868

Type Locality: Repulse Bay, North West Territories.

O. m. gibsoni Holland, 1931

Type Locality: Kuskoquim River Valley, Alaska.

O. m. lucilla Barnes and McDunnough, 1918

Type Locality: Hall Valley, Colorado.

* O. m. beani Elwes, 1893

Type Locality: Laggan, Alberta (Lake Louise).

O. m. semidea (say, 1828)

Type Locality: White Mountains, New Hampshire.

Notes

North of the type locality, specimens of O. m. beani, while appearing phenotypically identical to southern specimens, live in a

different habitat. Southern populations are restricted to areas of rock covered by black lichens. In the north, they are found on stable talus slopes where there is no black lichen.

Distributions of the seven subspecies are indicated in Figure 20. Geographical limits of the arctic subspecies are uncertain. This species is recorded from Alaska, the Yukon Territory, arctic North West Territories excluding the high arctic islands, Quebec, Manitoba, Labrador and Newfoundland, British Columbia, Alberta, Montana, Wyoming, Utah, Colorado, New Mexico, and New Hampshire. Alberta distribution is indicated in Figure 39.

Material examined: 73 specimens.

5.16 Oeneis polixenes (Fabricius, 1775) #671

Six subspecies are recognized.

O. p. polixenes (Fabricius, 1775)

Type Locality: Labrador? "America Boreali".

O. p. subhyalina (Curtis, 1835)

Type Locality: Boothia Peninsula, North West Territories.

O. p. katahdin (Newcomb, 1901)

Type Locality: Mount Katahdin, Maine.

O. p. peartiae (Edwards, 1897)

Type Locality: Winter Cove, Cambridge Bay, North West Territories.

* O. p. brucei (Edwards, 1891)

Type Locality: Bullion Mountain, Hall Valley, Park County,

Colorado.

O. p. yukonensis Gibson, 1920

Type Locality: unavailable.

Notes

There appears to be a gap in the distribution of O. p. brucei. It is not reported from Montana or southern Alberta. O. b. edwardsi shows a similar gap. These two species are very similar, and in both, adults fly early in the season. It is possible that this gap represents a temporal collecting bias, and not an actual disjunction.

O. p. brucei was first collected in Alberta in the vicinity of Banff. Adults are more commonly encountered north of Banff than south. This species has not been reported from southern British Columbia, being restricted, like O. b. edwardsi, to the front ranges east of the Rocky Mountain Trench.

Geographical Distribution

Distribution is indicated in Figure 21. This species has been reported from Alaska, the Yukon Territory, arctic North West Territories excluding the high arctic islands, Quebec, Manitoba, Labrador, northern British Columbia, Alberta, Wyoming, Colorado, and Maine. Alberta distribution is indicated in Figure 40.

Material examined: 222 specimens.

5.17 Erebia magdalena Strecker, 1880 #675

Two subspecies are recognized.

E. m. magdalena Strecker, 1880

Type Locality: Mountains near Georgetown, Colorado.

E. m. mackinleyensis Gunder, 1932

Type Locality: Sable Pass, Mount Mckinley National Park, Alaska.

Notes

In spite of intensive collecting, this species has not been reported from north of the Beartooth Plateau, Montana, or south of the Yukon Territory. The two subspecies are fairly distinct.

Geographical Distribution

Distribution is indicated in Figure 22. This species is known from Alaska, the Yukon Territory, Montana, Wyoming, Utah, Colorado, and New Mexico.

Material examined: 25 specimens.

5.18 Erebia fasciata Butler, 1868 #676

Two subspecies are recognized

E. f. fasciata Butler, 1868

Type Locality: Victoria Island, North West Territories.

E. f. avinoffi Holland, 1930

Type Locality: Kotzebue Sound, Alaska.

Geographical Distribution

Nearctic distribution is indicated in Figure 23. This species is known from Alaska, the Yukon Territory, and arctic North West Territories excluding the high arctic islands and Baffin Island. It is also

recorded from Asia.

Material examined: 25 specimens.

5.19 Erebia youngi Holland, 1900

Three subspecies are recognized.

E. y. youngi Holland, 1900

Type Locality: Mountains between 40 mile and Mission Creeks, Alaska.

E. y. herscheli Leussler, 1935

Type Locality: Herschel Island, Yukon Territory.

E. y. rileyi dos Passos, 1947

Type Locality: Mount McKinley National Park, Alaska.

Notes

Adults of this species are easily confused with those of E. dabanensis; records of one may easily refer to the other.

Geographical Distribution

Distribution is indicated in Figure 24. This species is also recorded from Asia. In North America, it is found in Alaska, and Yukon Territory, and western-most arctic North West Territories.

Material examined: 12 specimens.

5.20 Erebia dabanensis Erschoff, 1871

Type Locality: Chamar-daban, Urkutsk, U.S.S.R.

Notes

This species has tentatively been identified from a number of localities in Alaska. The specimens may represent E. youngi. Details for their separation are given in Warren (1936).

Geographical Distribution

Distribution is indicated in Figure 25. So far, this species has only been reported from Alaska and eastern Asia.

Material examined: 1 specimen.

5.21 Erebia inuitica Wyatt, 1966

Type Locality: Anaktuvuk Pass, Alaska.

Notes

This species has not been collected since its description.

Geographical Distribution

The type locality is indicated in Figure 26.

5.22 Erebia callias Edwards, 1871 #681

Type Locality: Colorado.

Notes

E. callias is common in the southern Rocky Mountains. It is the only endemic butterfly in the southern Rocky Mountains that is restricted to tundra.

Geographical Distribution

Distribution is indicated in Figure 27. It is recorded from Montana, Wyoming, Utah, and Colorado. It has also been reported from Asia.

Material examined: 23 specimens.

5.23 Analysis of distribution patterns

This section contains a brief discussion of some trends indicated by distribution patterns shown by the tundra butterflies in North America. These trends will form the basis for the examination of the Alberta tundra butterfly fauna.

5.23.1 Areas of species concentration

Table 1 indicates that two areas of concentration of tundra butterfly species can be identified. There are 16 species from Beringia; more than in any other area of North America. The other area of concentration is the Rocky Mountains, particularly along the front ranges. Fourteen species are known from this area.

These two areas are also the only areas which support endemic species; each area has five. This suggests that the fauna of each area has evolved independently, but with several imcomplete faunal interchanges. This is discussed in more detail later.

It is significant that these two areas are the only major alpine areas of which parts were not glaciated during the Pleistocene.

5.23.2 Faunal relationships

Area outside the limits of the two centers of diversity support fewer tundra species as the distance from the centers of diversity increases. The three areas with the fewest species are also the areas farthest away from, or most isolated from the centers of diversity. Figure 28 summarizes these trends.

Three major subtraction patterns can be identified. The first is from Beringia north east to the high arctic islands. The second is

TABLE 1: DISTRIBUTION PATTERNS OF NEARCTIC TUNDRA BUTTERFLIES

Fig. No.	Species	Area of Occurrence: BER Yuk-Al	WHB	EHB	ENA	LAI	HAI	RM	CR
5	P. eversman.	X							
6	C. boothi	X	X			X			
7	C. nastes	X	X	X		X	X	X	
8	L. phleas	X	X			X	X	X	X
9	L. snowi							X	
10	E. editha							X	X
11	B. napaea	X	X			X		X	
12	B. improba	X	X			X		X	
13	B. polaris	X	X	X		X	X		
14	B. alberta							X	
15	B. astarte							X	
16	B. distincta	X							
17	B. eunomia							X	
18	O. bore	X	X	X	X	X		X	
19	O. melissa	X	X	X	X	X		X	
20	O. polixenes	X	X	X	X	X		X	
21	E. magdalena	X						X	
22	E. fasciata	X	X			X			
23	E. youngi	X							
24	E. dabanensis	X							
25	E. inuitica	X							
26	E. callias							X	
	Totals	16	10	5	3	10	3	14	2
	Unique species	5	0	0	0	0	0	5	0

Abbreviations
Yuk-Al - Yukon Teritory and Alaska
WHB - Western Hudson Bay
EHB - Eastern Hudson Bay
ENA - Eastern North America (New England Area)
LAI - Lower Arctic Islands
HAI - High Arctic Islands
RM - Rocky Montains
CR - Coastal Ranges
BER - Beringia

from Beringia to isolated tundra in eastern North America. The third is from the Rocky Mountains to the Sierra of California.

5.23.3 Diversity

While there are a number of butterfly species in North America restricted to tundra, they are classified in only seven genera. This represents a rather impoverished generic fauna compared with other community types. None of these genera are restricted to tundra. This is part of a general pattern seen in most of the tundra biota, and is probably due to the young age of this community type.

5.23.4 Discussion

The subtraction patterns mentioned above are the result of the inability of most species found at the centers of diversity to disperse to distant isolated areas, particularly in post Wisconsin times. This is discussed in more detail later.

Dispersal of tundra butterflies in North America can best be described as a slow process, as evidenced by the subtraction patterns described above. It has occurred in orderly steps since the onset of the Pleistocene. The major source area was Beringia, with some species entering the southern Rocky Mountains early in the Pleistocene. In response to vacant niches in these mountains, endemic taxa developed here later in the Pleistocene. These do not appear to have had sufficient time to disperse into arctic habitats.

Alberta is situated in a position which is geographically intermediate between the two centers of diversity. Its tundra butterfly fauna is composed of elements derived from both. Because of the effects

of the last Pleistocene glaciation, analysis of its butterfly fauna presents an important opportunity to assess the effects and extent of interchange between two major Wisconsin refugia.

5.24 Distribution of tundra butterflies in Alberta

Twelve taxa are known from Alberta. Their distributions are shown in Figures 29 through 40. These taxa are:

C. n. streckeri Figure 29
L. p. arethusa Figure 30
L. s. snowi Figure 31
E. e. beani Figure 32
B. n. reiffi Figure 33
B. l. youngi Figure 34
B. alberta Figure 35
B. astarte Figure 36
B. e. nichollae Figure 37
O. b. edwardsi Figure 38
O. m. beani Figure 39
O. p. brucei Figure 40

5.24.1 Distribution Patterns

These twelve taxa are grouped into four types of distribution patterns: Southern Montane, Central Montane, Disjuncts, and Endemics.

5.24.1.1 TYPE 1 - Southern Montane (Figure 41a)

This pattern includes five taxa whose ranges extend from Alberta south to the Montana-Wyoming border, or beyond to Colorado and New Mexico.

L. p. arethusa
O. p. brucei
L. s. snowi
O. b. edwardsi
O. m. beani

5.24.1.2 TYPE 2 - Central Montane (Figure 41b)

This group includes four taxa not found north of the British Columbia-Yukon Territory border, or south of northern-most Montana and Washington.

C. n. streckeri
E. e. beani
B. alberta
B. astarte

5.24.1.3 TYPE 3 - Disjuncts (Figure 41c)

One taxon found in Alberta represents a disjunction from a northern

population. There do not appear to be any disjunctions from southern populations.

B. i. youngi

5.24.1.4 TYPE 4 - Endemic forms (Figure 41d)

Included here are two taxa known only from the central Canadian Rocky Mountains.

B. e. nichollae B. n. reiffi

Possibly three other taxa may be placed here. As mentioned earlier, the Alberta population of Boloria improba may represent an undescribed subspecies. Also, O. m. beani from around Prospect Mountain shows an ecological specialization which may deserve recognition, and the one specimen of L. p. arethusa from above treeline at Prospect Mountain is very different from normal arethusa. This may be an aberration, or it may represent an undescribed taxon.

CHAPTER 6. ANALYSIS OF DISTRIBUTION PATTERNS

6.1 Introduction

In this section, I provide explanations for the observed distribution patterns of the tundra butterflies of Alberta. In general, distribution patterns are determined in part by ecological tolerances, or proximal factors, and in part by past events, or historical factors (Udvardy, 1969; Larsen and Barry, 1974; Löve and Löve, 1974). I have not attempted to study explicitly by experimental means those factors involved with ecological tolerance. Rather, I accept that such exist, and assume that the tundra butterflies of Alberta exist in such areas because the latter are favorable. Further, I assume that these taxa do not live elsewhere in geographically proximal areas, because they cannot tolerate other ecological conditions, either biotic or physical. I concentrate on explaining the historical concomitants of the distribution patterns.

In general, historical explanations depend on a series of hypotheses, because the determining events were not observed, and thus their existence and interrelations must be inferred from evidence that is presently available. However, meaningful inferences cannot be generated *in vacuo*. Rather, they are based on assumptions that must be regarded, for the sake of a given set of circumstances, as axiomatic. My assumptions are as follows.

1. Climatic events of the Wisconsin glacial stages influenced the distribution patterns of extant butterfly taxa of tundra areas of Alberta. There is a vast amount of data which document the effects of this glaciation on other groups of animals and plants. For the present, these

effects are assumed for the tundra butterflies as well. Specific indications derived from distribution patterns shown by tundra butterflies are discussed in the section on source areas of this fauna.

2. Unglaciated areas of the eastern slopes of the Rocky Mountains were habitable during glacial times.

This assumption is neccessary to explain the presence of disjunct populations of non-butterfly taxa in the study area, given that these disjunctions are not artifacts and are interpreted correctly. Geological data mentioned earlier indicate the likelihood that this assumption is valid.

3. Immediate ancestral stocks of all species of butterflies that are included in each distribution type survived together in the same refugium.

This assumption is required to explain the fact that more than one taxon shows a given distribution pattern.

4. Dispersal of tundra adapted stocks has been slow and orderly. This has been the result of the non-randon and gradual retreat of Wisconsin ice sheets. Because life spans are short, and flight capabilities are generally poor, tundra butterflies do not appear to be suited to dispersal over long distances.

5. Evidence of endemism is evidence of isolation of such stocks from other populations for a period of time that extends from the present to at least the end of the Sangamon interglacial stage.

Genetic change usually requires a period of isolation (see Morisset, 1971, and Packer, 1971, for discussions in the context of endemism and refugia). Endemism is one way that such genetic change is expressed. The end of the

Sangamon interglacial is the last possible time that endemic populations could have been genetically continuous with ancestral populations of other forms.

Explanation of the distribution patterns of the tundra butterflies of Alberta requires postulation of source areas of these populations. There are three potential source areas: Beringia, Continental North America south of Wisconsin ice, and one or more refugia within the limits of continental ice along the Rocky Mountains in Alberta and British Columbia. Two are external to Alberta: Beringia, and Continental North America south of Wisconsin ice. One includes the eastern slopes of the Rocky Mountains, that is, an internal refugium in the sense that it was probably surrounded by ice at the height of the Wisconsin glacial stage.

Existence of the external source areas is well established by an abundance of evidence. Existence of the internal source area is based on less extensive evidence: at least twelve plant taxa have disjunct populations in the front ranges of the Rocky Mountains (Packer and Vitt, 1974), as do three species of beetles (Belicek, 1976; Ball, personal communication), and one crustacean. The endemic species of crustacean which has been reported (Clifford and Bergstrom, 1976) is of questionable value in this context.

6.2 The Albertan refugium

Extensive areas surrounded by ice were probably available in Alberta during Wisconsin time for habitation, although much of the unglaciated area was likely bedrock, and probably too rugged and too high to support tundra vegetation. Today, distribution of disjunct taxa is concentrated

along the front ranges of the Rocky Mountains, and especially in the Mountain Park area. Endemic taxa are also centered in this area. Possibly the refugium was located in this area during the Wisconsin stage.

Figure 42 indicates the approximate limit of Wisconsin ice in the Mountain Park area. A high ridge on the western side, which now forms the Jasper National Park boundary, would have prevented ice from entering this area from the west. The northern boundary has been documented as Cordilleran ice in the Athabasca River Valley which coalesced with Laurentide ice in the vicinity of Hinton (Roed, Mountjoy and Rutter, 1967). See Figure 5. The eastern boundary would most likely have been somewhere in the foothills, or the eastern slopes of Cadomin and Red Cap Mountains. The southern boundary is uncertain, and the refugium may have extended south to Nordegg, where ice in the Saskatchewan River valley would have formed a barrier. The area encompassed is a series of valleys and ridges which run in an east-west direction. They provide, at present, considerable and varied alpine habitat. All ice present in the refugium during Wisconsin time would have been thin and of local derivation. It is probable that small pro-glacial lakes were present during the height of glaciation, being formed by summer melt waters off the ice and from annual snow fall. Alpine tundra could have maintained an extent and position similar to that at present.

6.3 Source areas of the Alberta tundra butterflies

Of the three possible source areas listed above, I believe that only two contained immediate ancestors of the extant populations under consideration. My major hypotheses, then, are:

1. The source area for butterflies with distribution types 1 and 2 was an external refugium south of the ice.

2. The source area for butterflies with distribution types 3 and 4 was an internal, or Albertan refugium.

Each of these hypotheses is discussed below. Additionally, a series of secondary hypotheses is presented in conjunction with locating more precisely the source area of the butterflies from the external refugium south of Wisconsin ice.

6.3.1 The source area for butterflies with distribution types 1 and 2

The source area of the nine taxa in these two groups is placed south of Wisconsin ice for the following reasons.

Of the nine species involved, five also live in Beringia, and are represented there by distinctive forms. Alberta material is easily allied with southern forms in all five species. None of the Beringian forms even approach the Alberta border to the north.

The remaining four species are not in Beringia, and two have clear relationships with southern taxa. This suggests that they evolved south of the Wisconsin ice sheets.

No tundra butterflies in Beringia have dispersed south into and still survive in Alberta.

In the Trichoptera (Nimmo, 1971) and Coccinellidae (Belicek, 1976) faunas that have been investigated, only a very small proportion has been derived from Beringia. This includes all habitat types. Of all Alberta's butterflies, the source area of only one can be identified as Beringia. This suggests that not only tundra elements, but all elements of the Beringian fauna could not easily migrate south, including the boreal

forest communities.

If these taxa survived Wisconsin glaciations in the Alberta refugium, there are a number of indications that might be expected.

First, we might expect that some of these taxa would have dispersed north from the refugium as well as south. There would not be barriers to entry into Alaska for the four species not present there now. We would also expect that some of the distinctly alpine taxa would be found on arctic tundra in the North West Territories. These possibilities have not been realized. It is possible that some of these taxa survived in the Alberta refugium, but have not contributed to colonization of other areas, however, in the absence of endemic tendencies, these cannot be identified.

It is also unlikely that taxa surviving in the Alberta refugium could have dispersed as far as New Mexico in post-glacial times, but not into the coastal ranges of Washington, Oregon, and California. This would imply long distance dispersal between mountain ranges, and the gaps are similar in size on the eastern and western mountain ranges.

In order to locate the source area of types 1 and 2 more precisely, the following hypotheses are made.

1. Taxa in types 1 and 2 survived the Wisconsin glaciation in the same refugium.

2. Dispersal south into Wyoming and Colorado from this refugium was blocked by gaps in habitat.

3. The tundra belt south of the ice sheet was very narrow and broken. This prevented dispersal east to New England and Quebec.

4. Dispersal west and south along the coastal ranges was blocked

by large gaps in habitat in central Washington.

These hypotheses are discussed below.

6.3.1.1 Taxa in types 1 and 2 survived together.

These taxa have similar boundaries on three sides of their present ranges. This indicates that they are responding to retreat of Wisconsin ice in a similar manner. If so, it is reasonable to expect that they would respond to the Wisconsin ice advances in a similar manner as well, and that as they were displaced south, and northern colonies were extinguished, the surviving colonies would be found in about the same area.

Type 1 distributions have been identified in plants (Packer and Vitt, 1974), Trichoptera (Nimmo, 1971), and Coccinellidae (Belicek, 1976). Type 2 distributions have been identified in Trichoptera (Nimmo, 1971), but not in plants or Coccinellidae. At least one species of carabid beetle shows this type of distribution: Nebria schwarzi. This indicates a fairly general phenomenon, and that large elements of the tundra community were involved. This is to be expected if the hypothesis is correct.

6.3.1.2 Dispersal from this refugium south was blocked by gaps in habitat.

This hypothesis is necessary to explain the fact that type 2 taxa have not dispersed farther south, where there appears to be ample suitable habitat, and empty niches available. Because there are no plant taxa which show this type of distribution, these butterfly taxa are not limited by foodplant distribution. It would seem that they have been physically blocked from dispersing south. The only reasonable explanation is that tundra was not very extensive, and that these taxa are not capable of crossing even minor gaps in habitat. In other words, dispersal can only be accomplished if the habitat is continuous. By hypothesizing a

narrow tundra belt, breaks would occur in the tundra belt in the vicinity of central Montana, which is where the barrier seems to have been.

Also in support of this hypothesis is the fact that the two endemic taxa in the southern Rocky Mountains have not been able to disperse north across this barrier.

It would appear that the presence of type 1 taxa in the southern Rocky Mountains would weaken this argument. However, because two of these taxa are derived from non-tundra species which evolved below the ice margin, their presence probably dates to pre-Wisconsin times. Also, because the three species on isolated tundra in New England and Quebec are also in the Rocky Mountains, they must either be capable of much better dispersal, or they must have had more time to reach these areas. While they may be more efficient at dispersing than other tundra butterflies, they have not managed to invade the arctic islands very successfully, which weakens the suggestion that they extended their ranges into the southern Rocky Mountains in post-Wisconsin times.

If they were present in North America during earlier, more extensive glaciations, not only would the extent of tundra be greater, and therefore the gaps smaller, but they would have had considerably more time to spread through the southern Rocky Mountains. It is suggested, therefore, that these taxa represent elements of an older dispersal south, perhaps during Illinoisan or Nebraskan glaciations. This might also explain the presence of E. magdalena and E. callias in Colorado and Wyoming.

6.3.1.3 The tundra belt along the southern margin of Wisconsin ice was discontinuous.

Six of the nine species under discussion are not represented in the

isolated tundra of New England and Quebec. The three tundra species there are represented by subspecies that are more closely related to subspecies in Labrador and the eastern arctic. This indicates that a major barrier was present. Because the six species that are absent inhabit a variety of habitats, and two of them inhabit all tundra areas except New England, Quebec, and the southern Rocky Mountains, it is reasonable to expect that the nature of this barrier had to be a break in the tundra belt. Otherwise, at least one or two of these species would be expected on the tundra in New England and Quebec, and the relationship would be closer between eastern and western populations of the three species found on both sides of this barrier.

Based on pollen core data, similar conclusions have been reached with respect to the discontinuous tundra belt (Löve, 1959; Ritchie, 1969; Wright, 1970).

6.3.1.4 Dispersal west and south along the coastal ranges was blocked by large gaps in habitat in central Washington.

Only two of the twelve species in Alberta are also on the coastal ranges, where each is represented by a different subspecies. Tundras from Oregon south to the Sierra Nevada are the most depauperate in terms of tundra butterflies, in North America. This indicates a major barrier. If minor barriers prove to be effective for these butterflies, distances between the mountain peaks in Oregon and southern Washington would be almost insurmountable. This is in keeping with the suggestion that the nine taxa in types 1 and 2 are unable to cross unfavorable habitat, and necessitates only one assumption to explain all boundaries and barriers encountered in this study.

It appears that tundra plants are also reacting to this barrier. According to Billings (1974), only 20% of the flora of the tundra of the Sierra Nevada has affinities with northern and arctic tundra floras. Of all known tundra in North America, this, and that of the Great Basin, are the most depauperate in arctic-alpine species.

The hypothesis seems to explain all the available data, while being contradicted by none. As more groups are investigated, particularly Carabidae, and the infraspecific relationships in the flora between the tundra areas discussed above, further tests of the hypothesis can be made.

The probable extent of the external refugium is indicated in Figure 43.

6.4 The source area for butterflies with distribution types 3 and 4

In this section, I discuss the validity of the assumptions that the distributions known for these taxa are accurate, and attempt to locate their source area.

6.4.1 Problems

The only taxon that shows a clear disjunction is B. improba youngi, which is represented in Alberta by a population disjunct from arctic Canada and Alaska. Collecting in the gap has been minimal, so there is a possiblity that this disjunction is an artifact, in which instance, this would represent the only dispersal into Alberta from the north in Post-glacial times. Because of the phenotypical differences between the Prospect Mountain population and the populations in the north, and because this species has not been found on the mountains in the vicinity

of Prospect Mountain, nor in the collections made north of Hinton, Alberta, I suspect that it probably represents a real disjunction. This would indicate either long distance dispersal, or survival in the area during the Wisconsin. Because of the distances involved (over 600 km.) it is unlikely that this represents long range dispersal. Adults of this species are very weak fliers.

Two taxa in type 4 may represent endemic forms. B. e. nichollae is very distinctive. B. n. reiffi is largely unknown. The type specimen appears to have been lost, and no specimens have been found that fit the type description. Alberta material has not been located. A short series from Pink Mountain, British Columbia has not been examined because of lack of material from the Yukon Territory and Alaska for comparison. This species must have been present before the Wisconsin glaciations because there is one disjunct population in Wyoming which represents a different subspecies.

6.4.2 Source area

The only feasible explanation for the presence of types 3 and 4 distributions is that these taxa survived at least the Classical Wisconsin glaciation in the Alberta Refugium.

Barriers to dispersal appear to be either lack of suitable habitat, or selection against dispersal during glaciations. This has been suggested for Carabidae (Lindroth, 1949).

6.5 Colonization of present day tundra in Alberta

In this section I will discuss the contribution and dispersal routes from each of the two refugia into Alberta tundra.

6.5.1 The Alberta Refugium

Dispersal of taxa which survived Wisconsin glaciations in this refugium has been minimal. B. i. youngi does not appear to have dispersed outside the boundaries of the refugium. B. e. nichollae has dispersed to areas within a 40 km. radius of Prospect Mountain, to areas west and south. B. n. reiffi is now located to the north of the refugium, which may indicate Post-glacial dispersal, or possibly that the refugium extended north of the Athabasca River Valley as a series of broken nunataks. If the ecological form of O. m. beani found in this area survived in the refugium, it has dispersed about the same amount as B. e. nichollae. This refugium does not seen to have contributed much to the colonization of Alberta tundra in Post-glacial times.

6.5.1 External refugium

As Wisconsin ice retreated, the tundra south of the ice is expected to have followed the ice margins north. As the tundra moved northward, the tundra butterflies would have as well. Boreal forest following behind the tundra would first invade the valleys, gradually isolating pieces of tundra on mountains. With the continued movement of both communities north, these isolated tundras would slowly move up the mountains to the summits as conditions for tree growth improved lower down. As ice retreated still farther, Laurentide ice withdrew to the east across the northern prairies and barrenlands of the North West Territories. The tundra belt followed the ice movements and boreal forest eventually replaced tundra in all the mountain valleys creating a series of isolated tundra communities on mountain summits. The breakup of continuous tundra effectively halted the dispersal north of tundra butterflies. The migration of the biota in

this refugium is summarized in Figure 43.

Because Cordilleran ice in northern British Columbia and the Yukon Territory did not break up until well after Laurentide ice had retreated eastward, Beringian flora and fauna were blocked from dispersing south by the presence of intact tundra and boreal forest communities derived from south of the ice sheets. In other words, the Beringian communities were blocked first by ice barriers, and later, by inter and intra specific competition.

6.6 Value of butterfly distributions in studies of refugia

It has been shown that two Wisconsin butterfly refugia can be identified in the Rocky Mountains of Alberta and adjacent areas. The first, Mountain Park, did not have much of a role in re-colonizing Alberta after the ice retreated. The second, northern Washington, Idaho, and Montana, was an important dispersal center for butterflies. Tundra butterflies are the only direct living indication that the tundra belt south of the ice margin was not continuous.

This suggests that the tundra butterfly fauna has an important potential as an indicator of refugia, and should be investigated whenever a study on the location of a refugium is undertaken.

6.7 Conclusions

The importance of refugia is twofold. They serve as centers of dispersal, and as centers for the development of new taxa. This study also suggests that large refugia tend to act as centers of dispersal, and that small refugia tend to serve as centers for the development of

new taxa.

Where areas surrounded by ice have been identified by geologists, evidence which indicates refugia has usually been found by biologists, but geologists cannot determine the limits of a given community type within the boundaries of an open, or continental refugium. Only investigation of the biological components can determine these limits with accuracy.

Figure 1.

Area encompassed by the topographical maps (Figures 29-40) of the Alberta Rocky Mountains and Foothills.

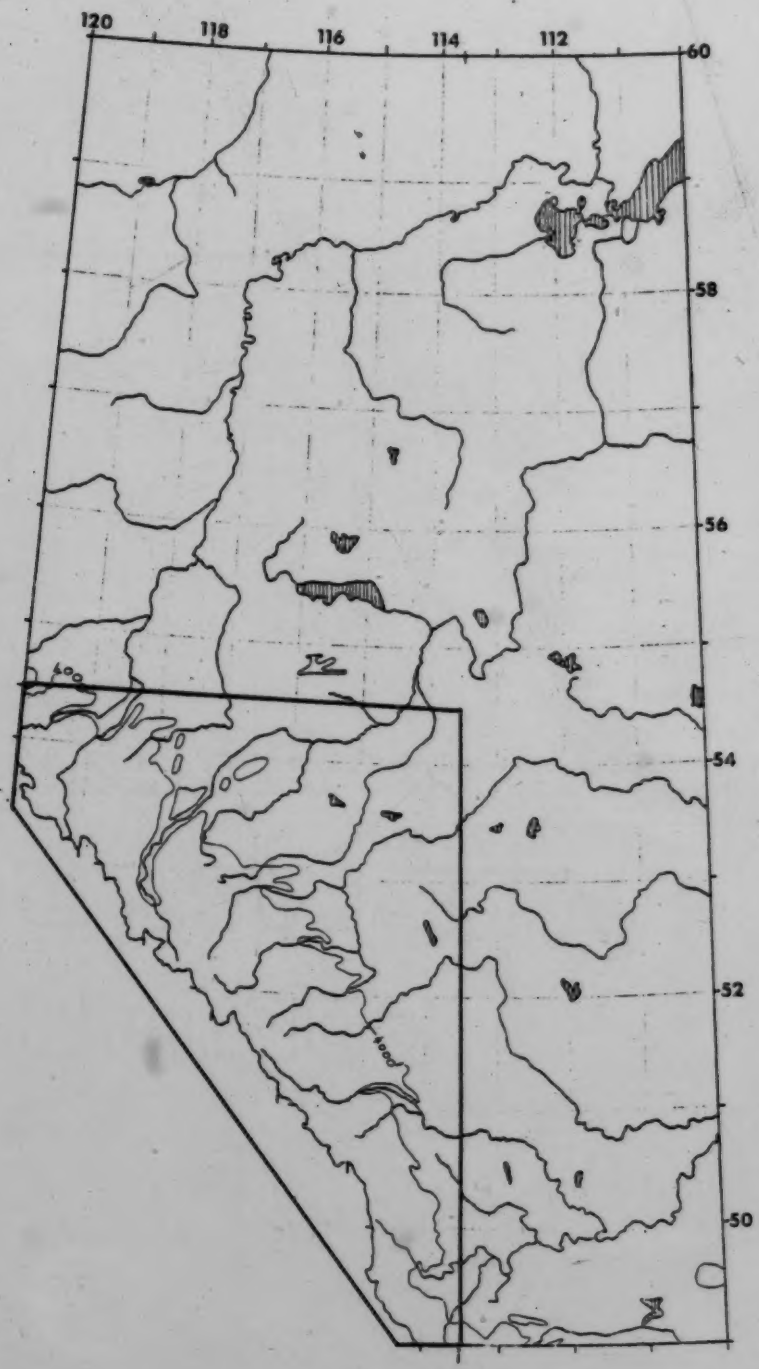

120
118
116
114
112
60
58
56
54
52
50
400
4000

Figure 2.

Correlations of Cordilleran tills in Alberta, from Reimchen and Bayrock (1977). Vertical columns are organized as follows. Author of study at the top, area of study next, and tills found in study area in order of increasing age. Correlations between tills are indicated by an equivalent horizontal position. Ages of these correllations are indicated on the left.

Geologic Time and Glacial Tills				Author	Roed et. al. 1967	Boydell 1972	Rutter 1972	Alley 1973	Reimchen and Bayrock 1977	
				Area	Hinton	Rocky Mountain House	Banff	Crowsnest	Rocky Mountains; Foothills	
	Recent				Drystone Creek		Eisenhower		Neoglacial 1, 2 Cirque	
	PLEISTOCENE	Wisconsin	Late		Obed Marlboro	Jackfish Creek Lamoral	Canmore Bow Valley	Hidden Creek	Young 7 Young 7b	Young 5
			Early		Valley glacier	Baseline	Pre-Bow Valley?	Maycroft	Intermediate 4	Intermediate 4b
		Sangamon Interglacial								
		Illinoisan Glaciation			Early Cordiller.	Hummingbird	"Erratics"	Albertan	Old 3	"Foothills Erratics"

Figure 3.

Extent of Wisconsin ice in selected areas of Alberta. Rectangles represent study areas, with the remainder of the Rocky Mountains and foothills insufficiently investigated. Within study areas, black represents ice, and white, unglaciated terrain. Uninvestigated areas within rectangles are marked by questionmarks. See Figure 2 for correlations between study areas.

A- after Roed, Mountjoy and Rutter, 1967; Marlboro advance.

B- after Curry, 1976; Marlboro and unnamed advances.

C- after Reimchen and Bayrock, 1977; tills 4 and 4b.

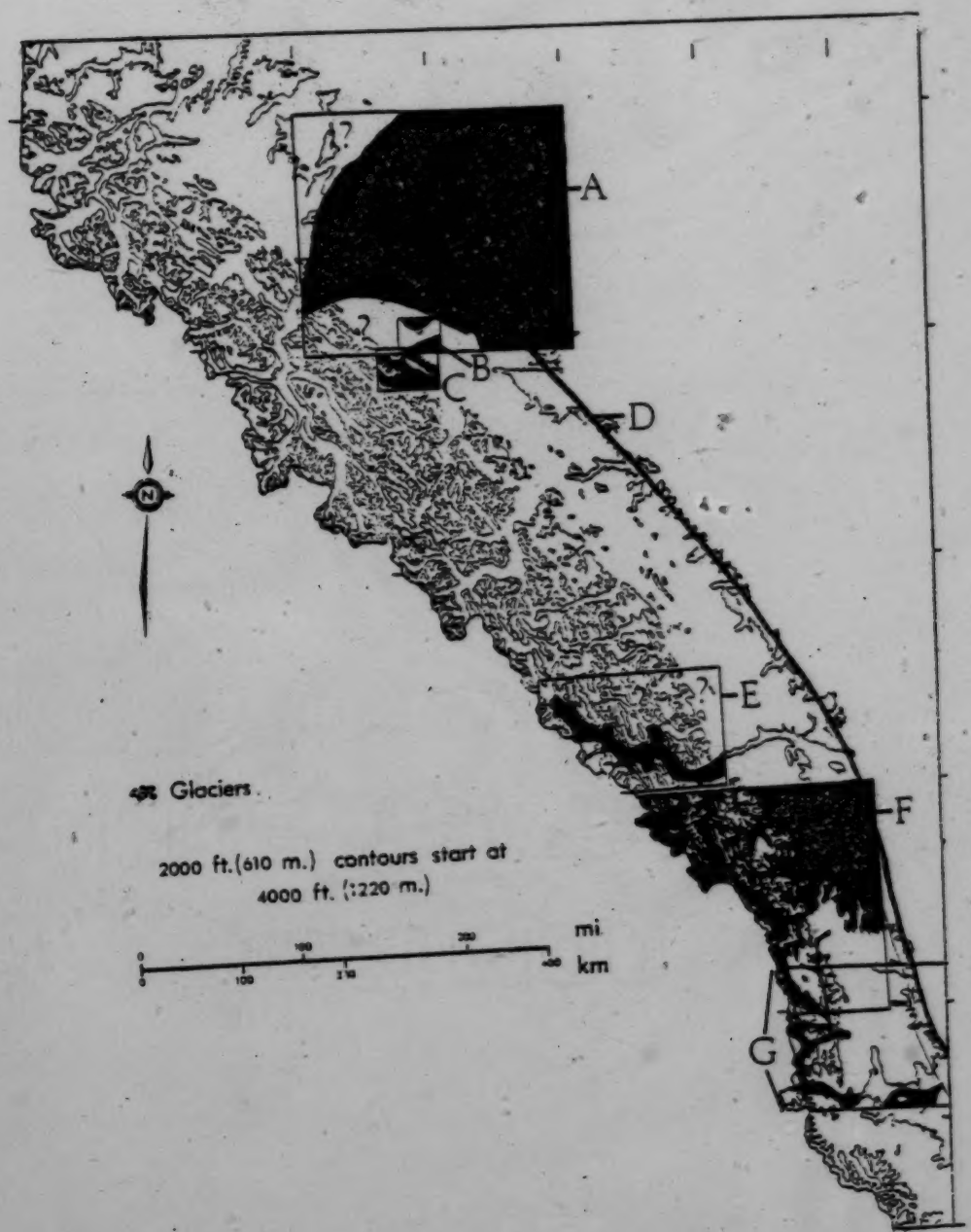
D- after Stalker, 1956; foothills erratics train; limit of western movement of Laurentide ice.

E- after Rutter, 1972; Bow Valley advance.

F- after Jackson, 1977.

G- after Allee, 1973; Maycroft advance.

Note that there appears to be ample unglaciated area and that where study areas overlap, hypotheses about the extent of ice are similar.


A
B
C
D
E
F
G
N
Glaciers
2000 ft.(610 m.) contours start at
4000 ft. (1220 m.)
mi
km

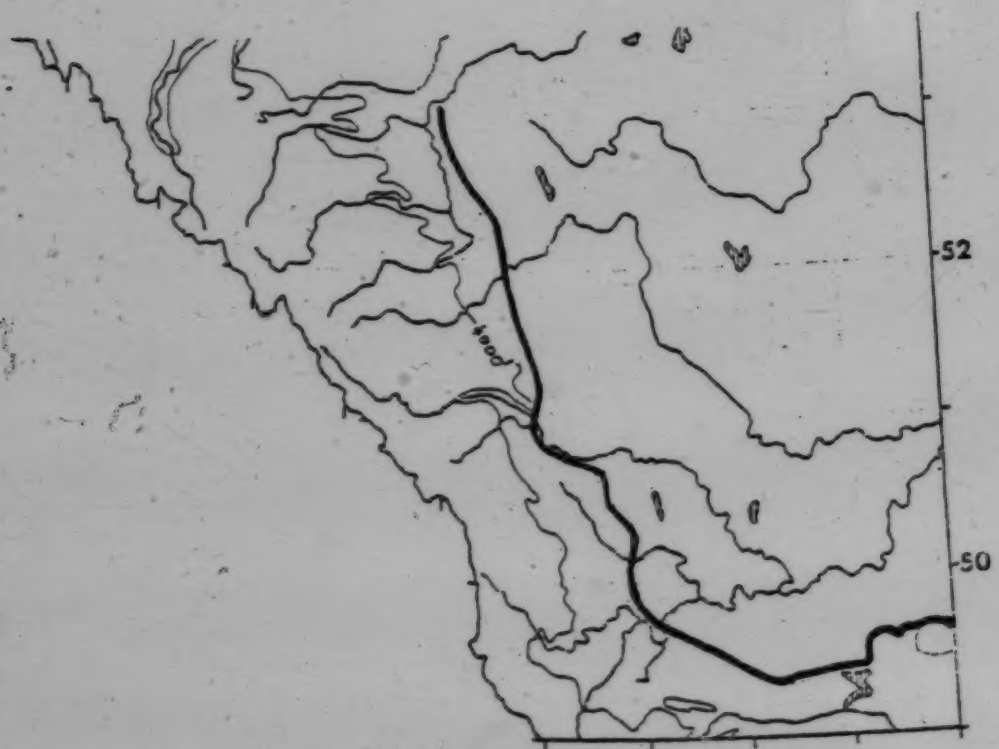


Figure 4.

Extent of Classical Wisconsin Laurentide ice in southern Alberta. After Stalker (1977). Ice is to the north east of the heavy line, which marks the limit of the advance.

Figure 5.

Important localities mentioned in the text.

A - Prospect Mountain (Mountain Park).

B - Shunda Mountain.

C - Coliseum Mountain.

D - Wilcox Pass.

E - Laggan (Lake Louise).

F - Hinton.

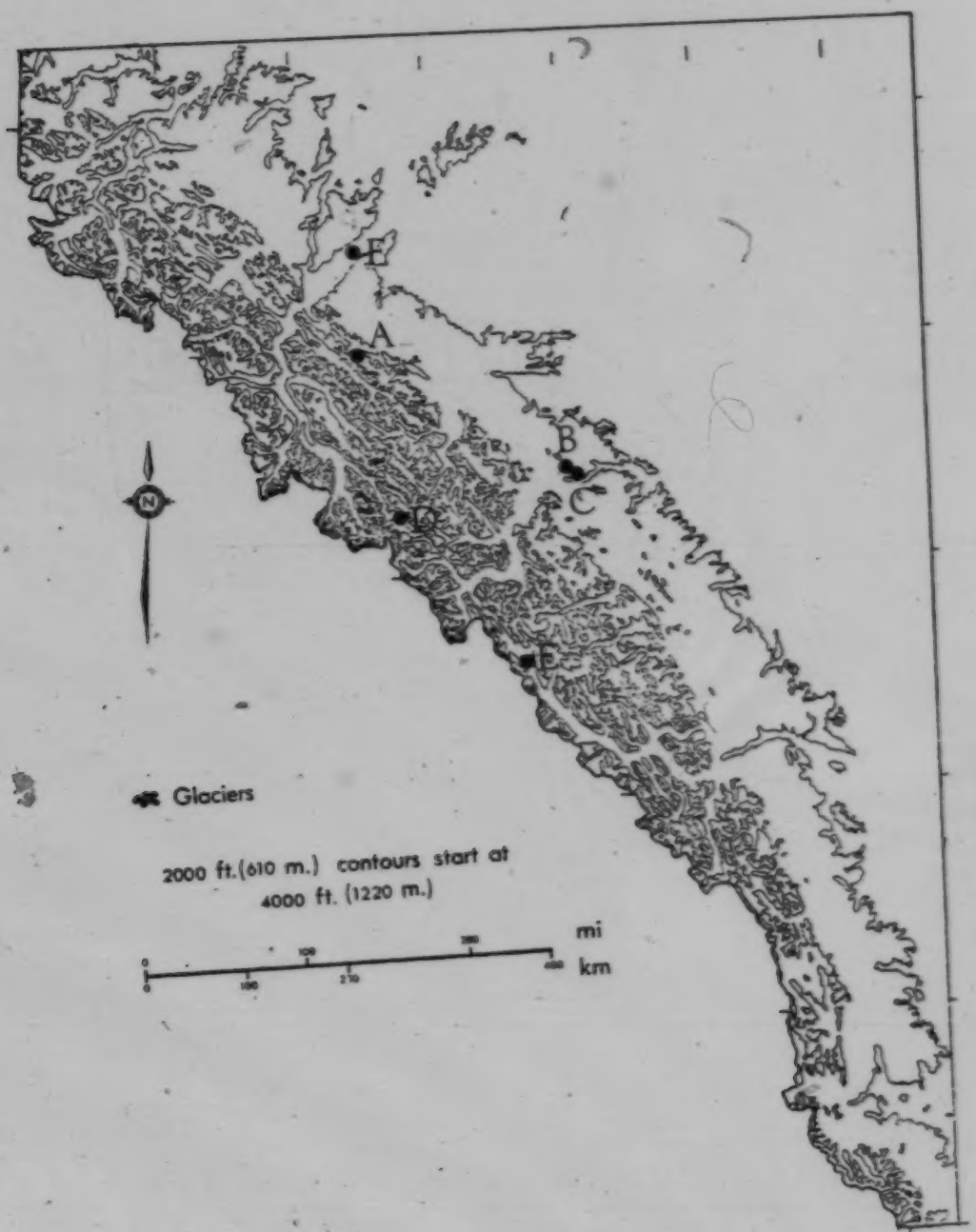

E
A
B
C
D
F
N
Glaciers
2000 ft.(610 m.) contours start at
4000 ft. (1220 m.)
mi
km

Figure 6.
Distribution of Parnassius eversmanni thor H. Edwards, 1881, in North America.

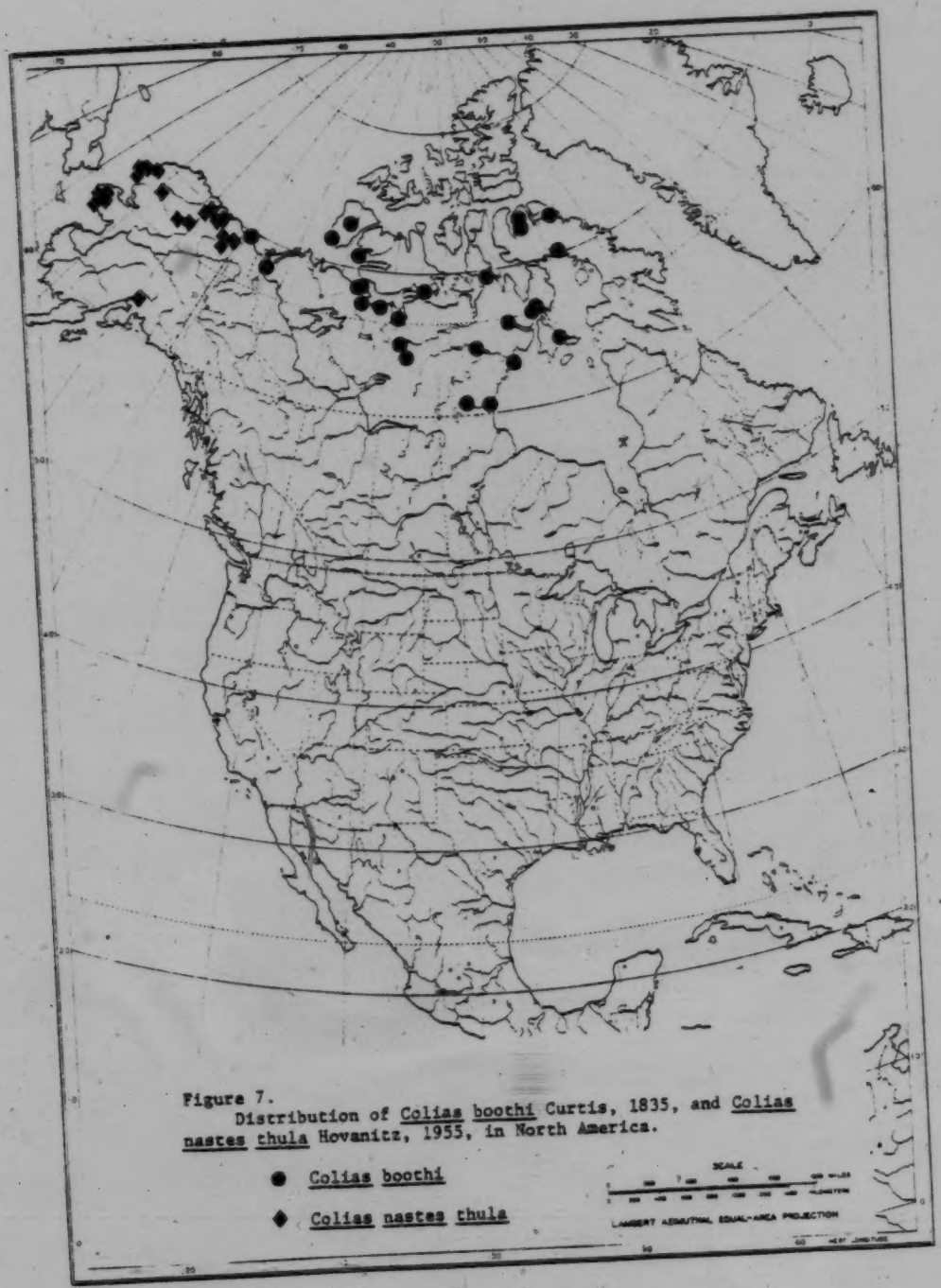


Figure 7.
Distribution of Colias boothi Curtis, 1835, and Colias nastes thula Hovanitz, 1955, in North America.

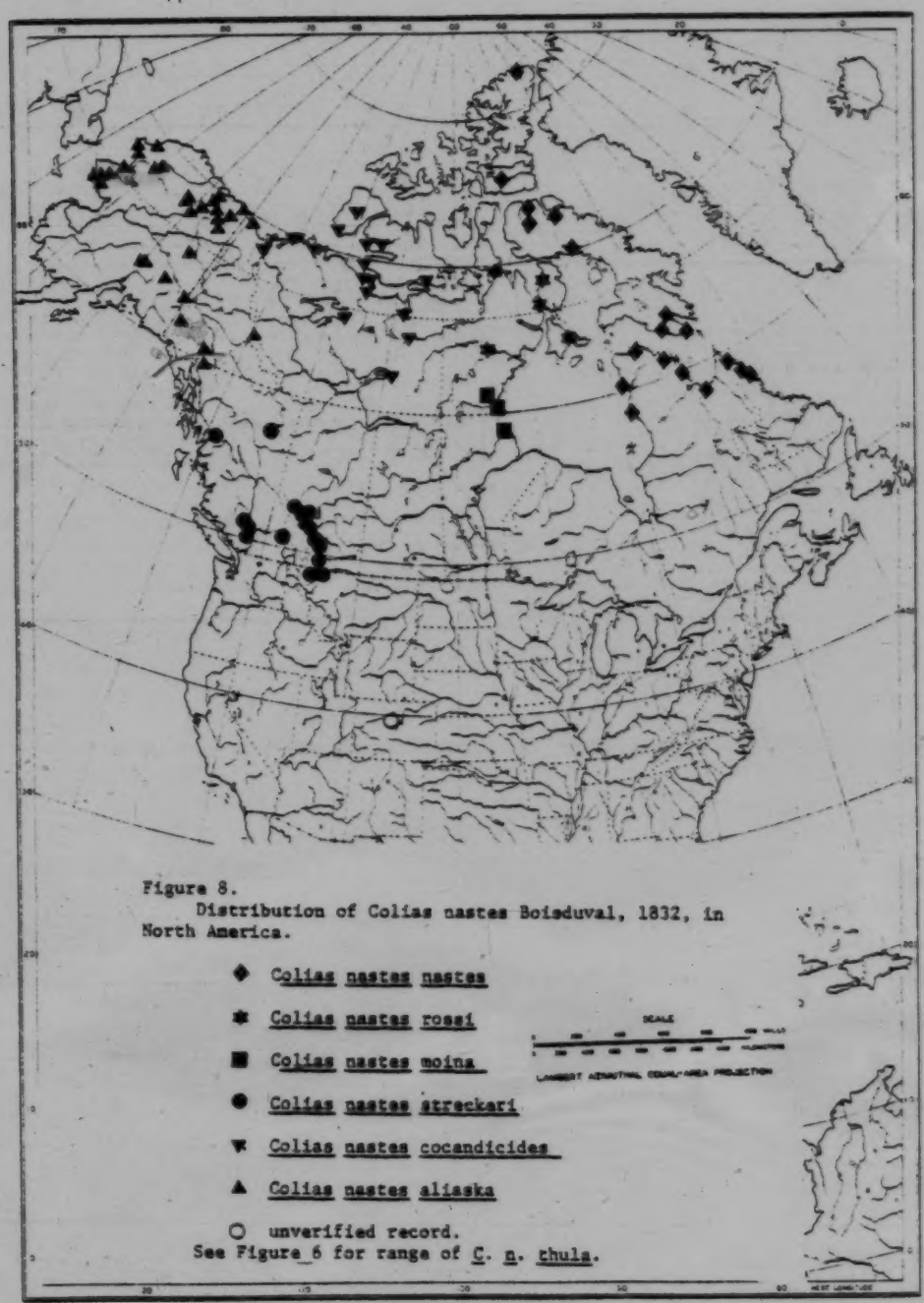


Figure 8.
Distribution of Colias nastes Boisduval, 1832, in North America.

◆ Colias nastes nastes

✱ Colias nastes rossi

■ Colias nastes moina

● Colias nastes streckari

▼ Colias nastes cocandicides

▲ Colias nastes aliaska

○ unverified record.

See Figure 6 for range of C. n. thula.

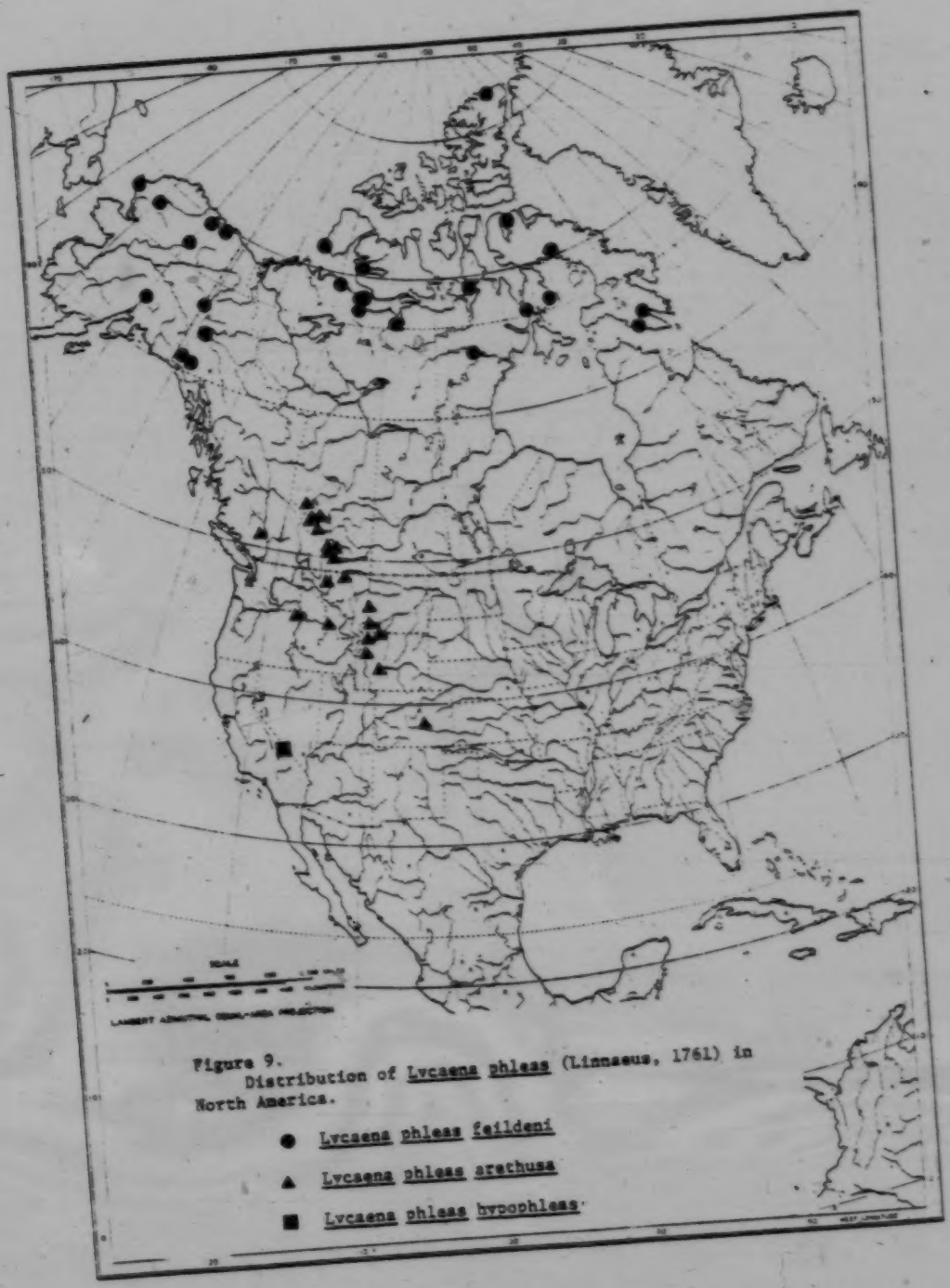


Figure 9.
Distribution of Lycaena phlaas (Linnaeus, 1761) in North America.

● Lycaena phlaas feildeni

▲ Lycaena phlaas arethusa

■ Lycaena phlaas hypophlaas

Figure 10.
Distribution of Lycaena snowi (Edwards, 1881) in North America.

● Lycaena snowi snowi

■ Lycaena snowi henrysa

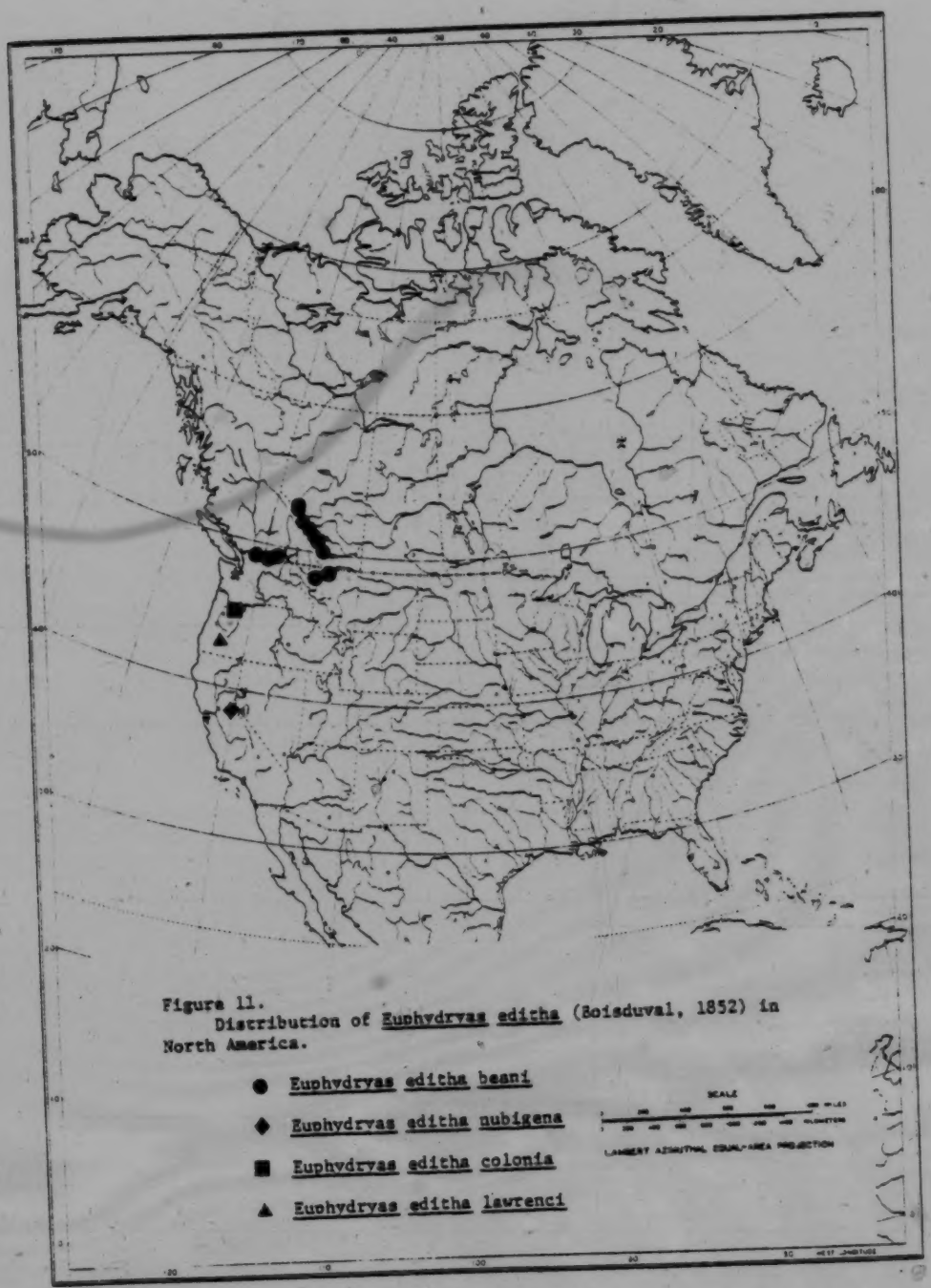


Figure 11.
Distribution of Euphydryas editha (Boisduval, 1852) in North America.

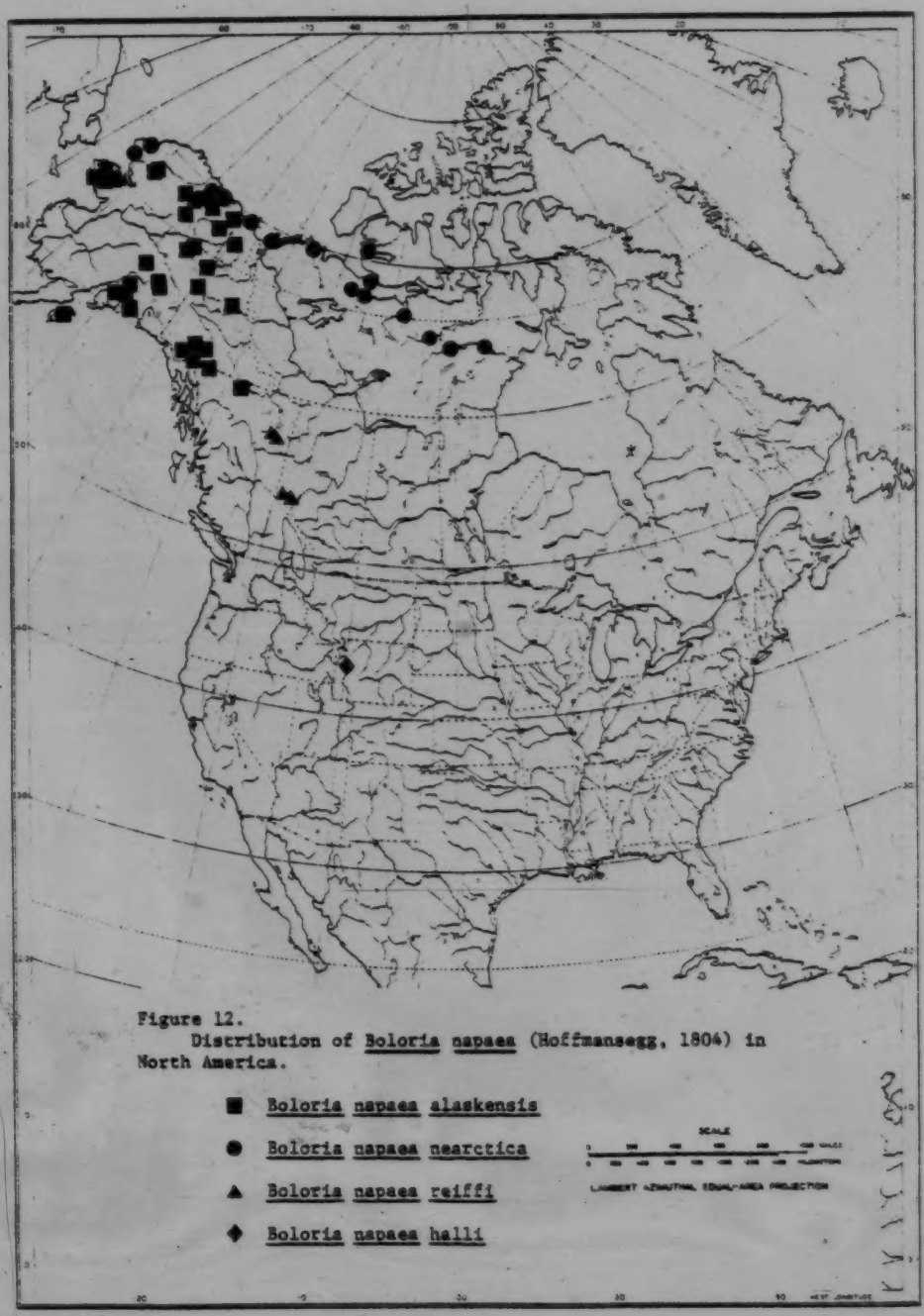


Figure 12.
Distribution of Boloria napaea (Hoffmansegg, 1804) in North America.

Figure 13.
Distribution of Boloria improba (Butler, 1877) in North America.

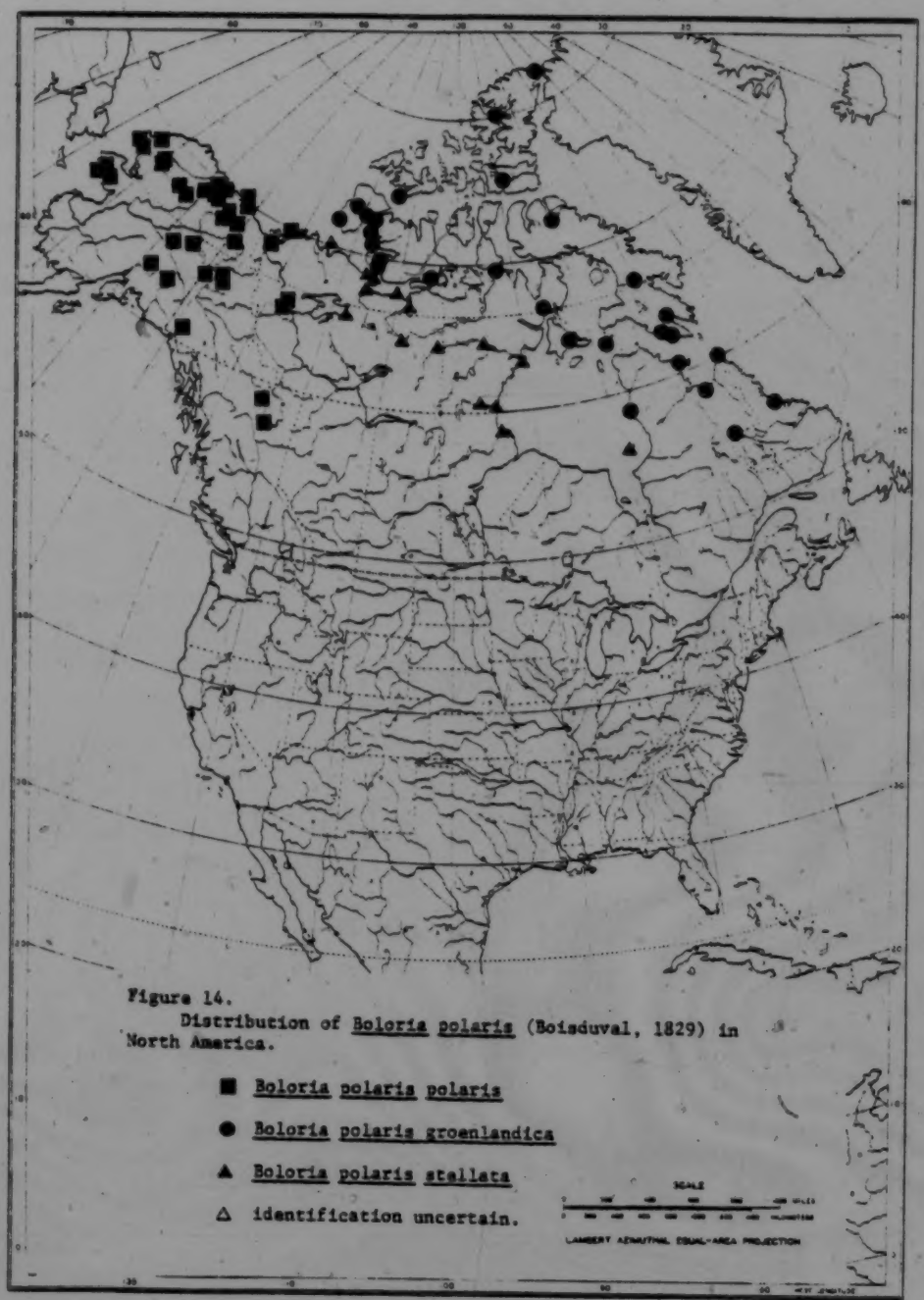


Figure 14.
Distribution of Boloria polaris (Boisduval, 1829) in North America.

Figure 15.
Distribution of Boloria alberta (Edwards, 1890) in North America. Open circle represents an unverified record.

Figure 16.
Distribution of Boloria astarte (Doubleday, 1847) in North America.

Figure 17.
Distribution of Boloria distincta (Gibson, 1920) in North America.

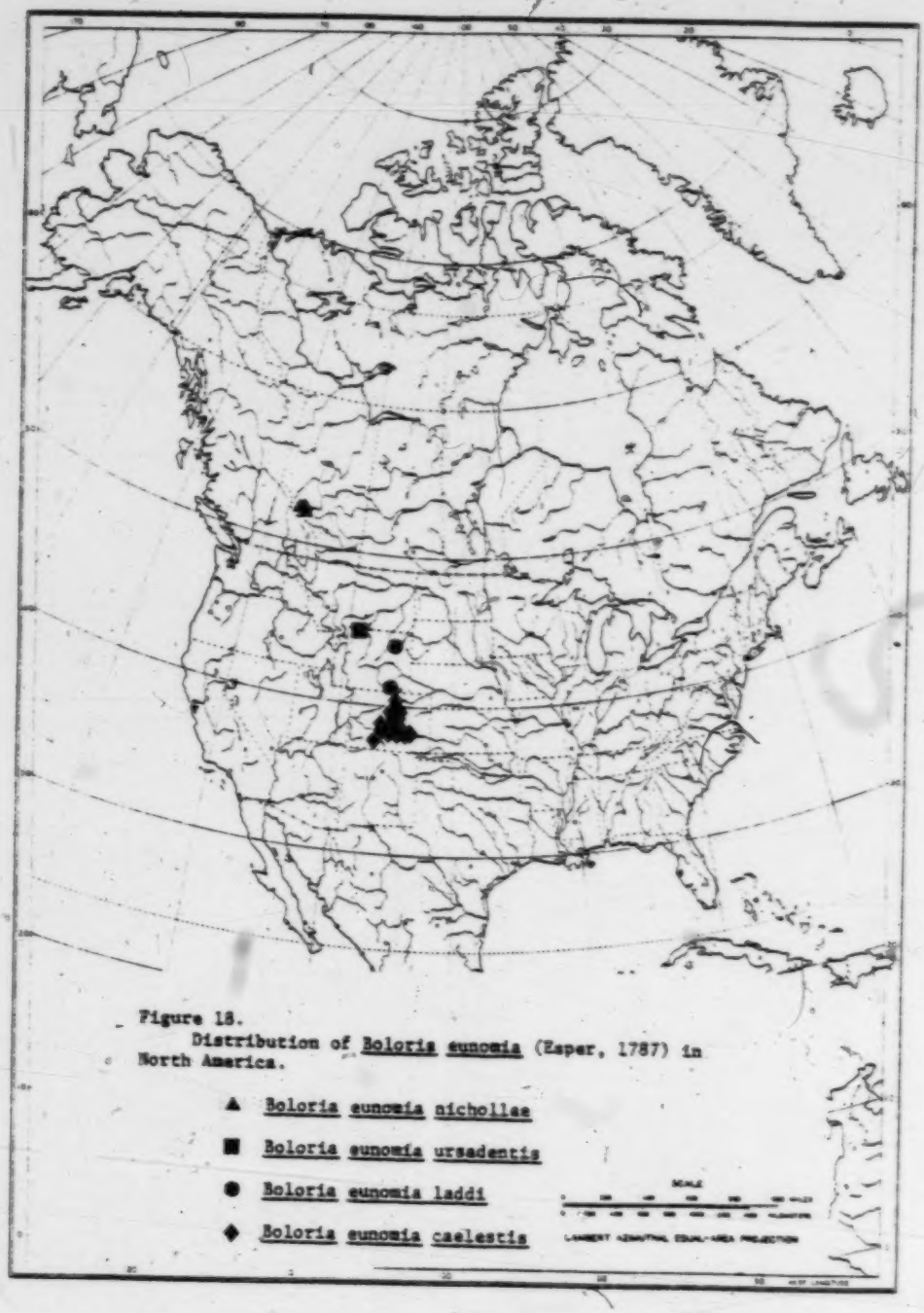


Figure 18.
Distribution of Boloria eunomia (Esper, 1787) in North America.

▲ Boloria eunomia nichollae

■ Boloria eunomia ursadentis

● Boloria eunomia laddi

◆ Boloria eunomia caelestis

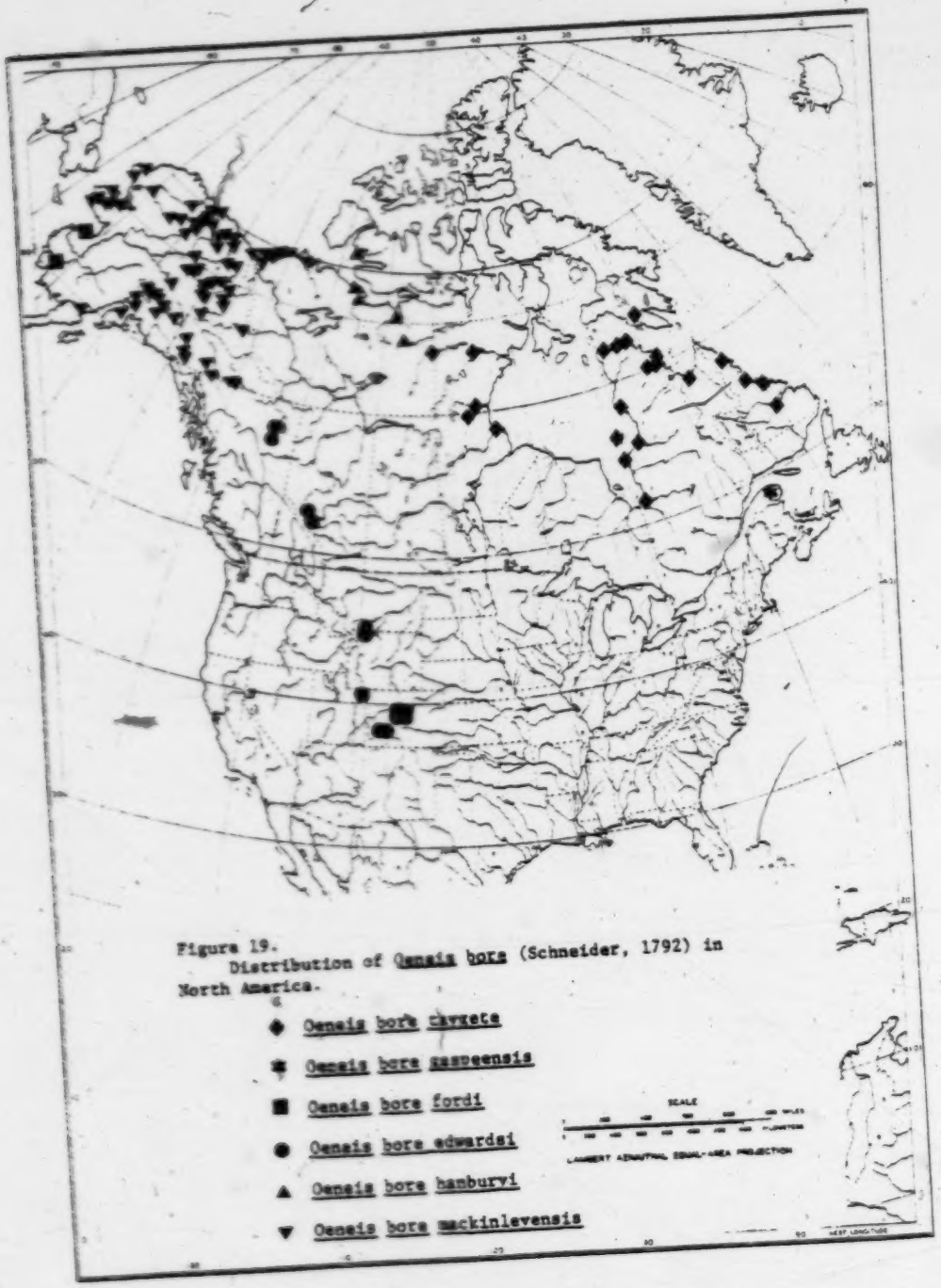


Figure 19.
Distribution of Oeneis bore (Schneider, 1792) in North America.

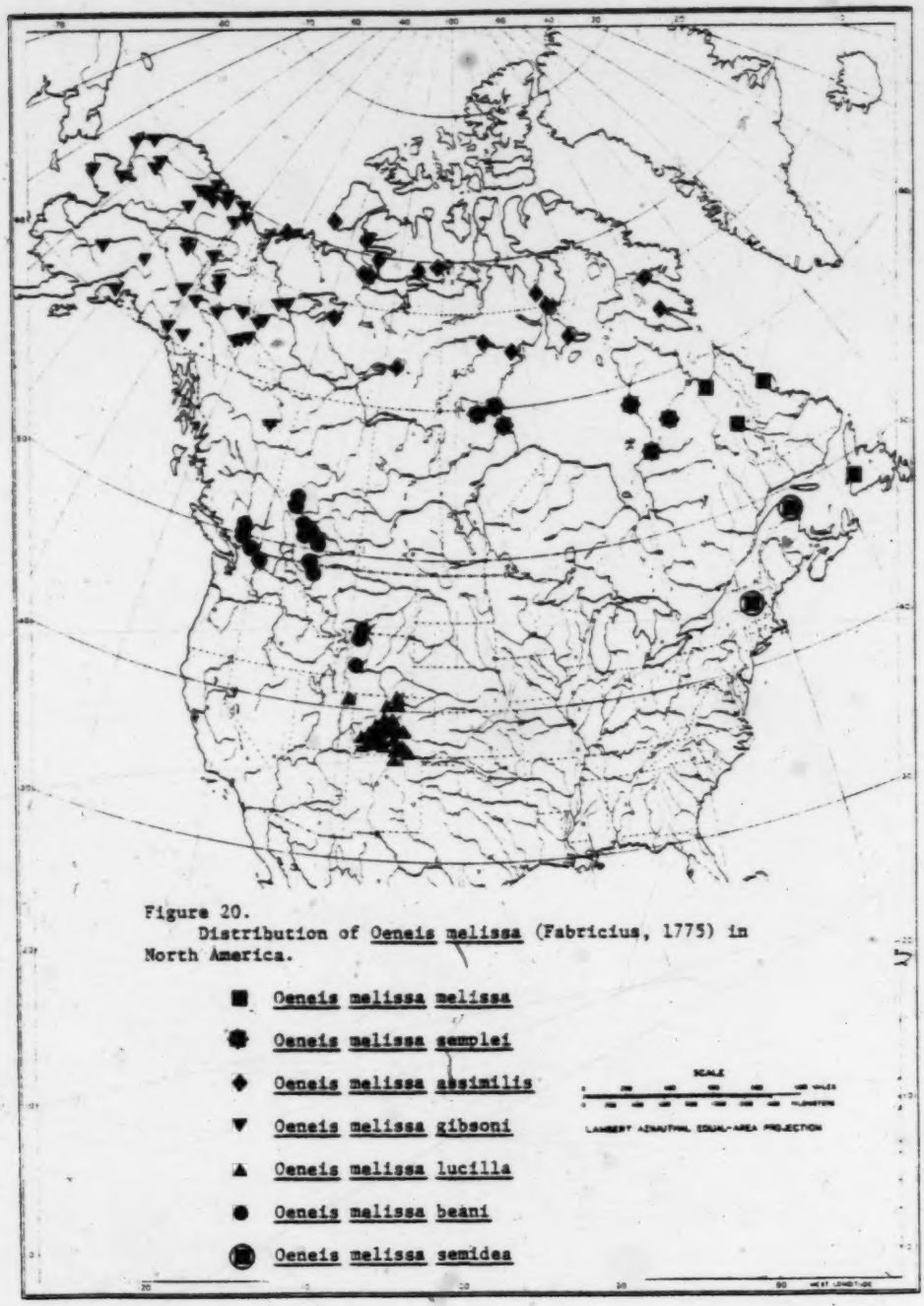


Figure 20.
Distribution of Oeneis melissa (Fabricius, 1775) in North America.

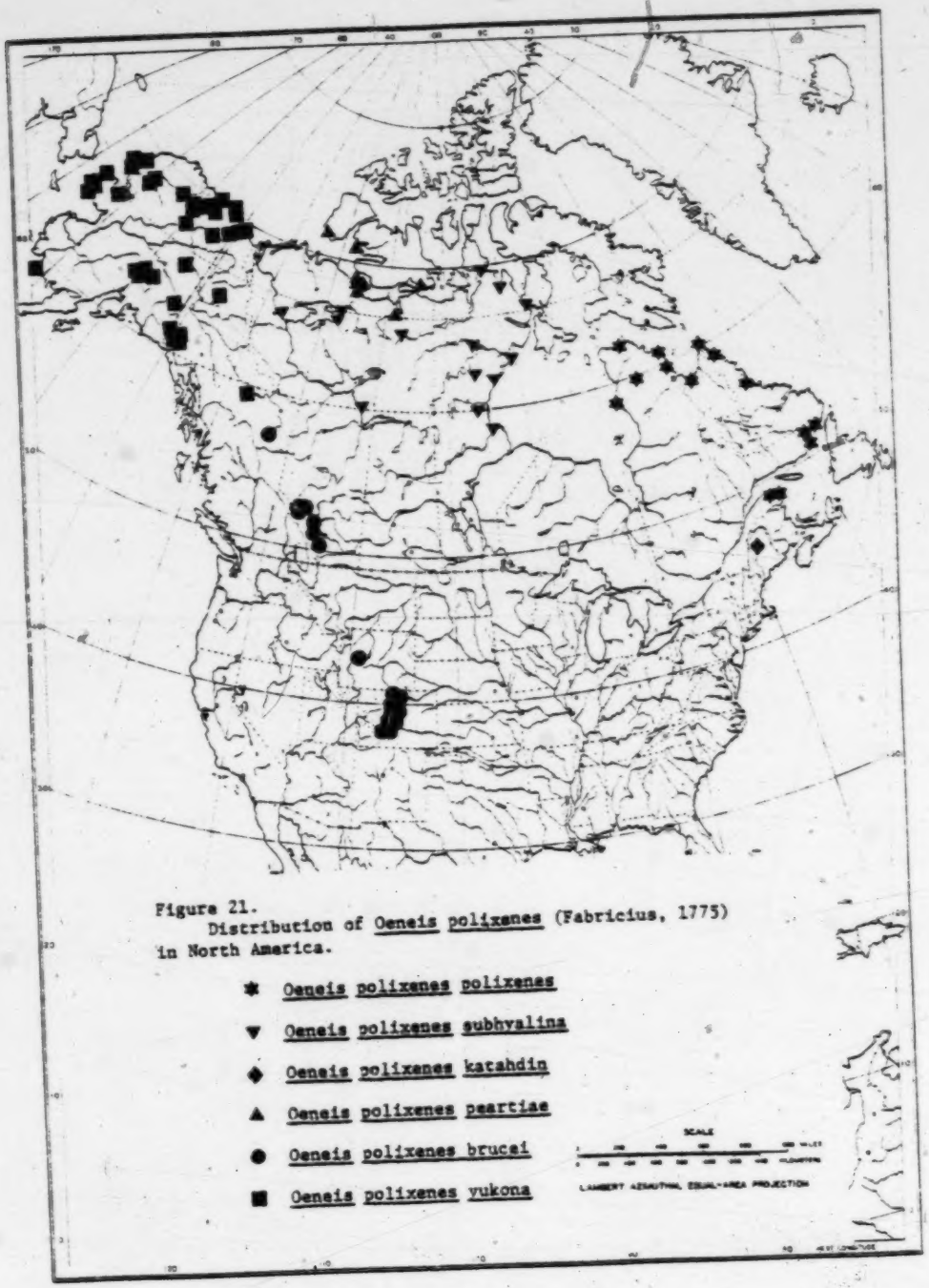


Figure 21.
Distribution of Oeneis polixenes (Fabricius, 1775) in North America.

Figure 22.
Distribution of Erebia magdalena Strecker, 1880, in North America.

▲ Erebia magdalena magdalena

● Erebia magdalena mackinleyensis

Figure 23.
Distribution of Erebia fasciata Butler, 1880, in North America.

● Erebia fasciata fasciata

▲ Erebia fasciata avinoffi

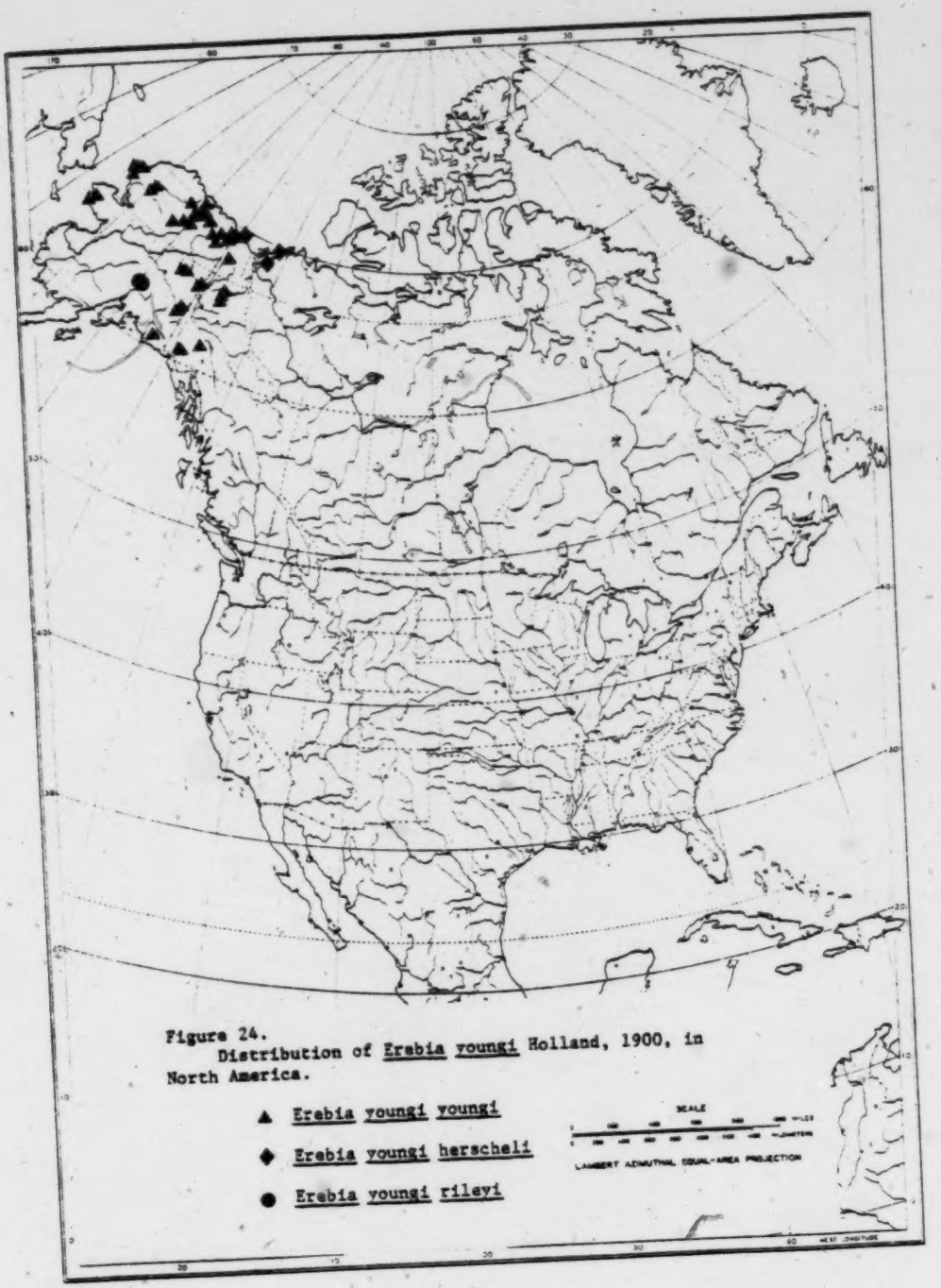


Figure 24.
Distribution of Erebia youngi Holland, 1900, in North America.

Figure 25.
Distribution of Erebia dabanensis Erschoff, 1871, in North America.

Figure 26.
Distribution of Erebia inuitica Wyatt, 1966.

Figure 27.
Distribution of Erebia callias Edwards, 1871, in North America.

Figure 28.

Subtraction patterns in the tundra butterfly fauna of North America. Numbers refer to numbers of species in each geographic area.

A - subtraction pattern from Beringia north east to Ellesmere Island and northern Greenland.

B - subtraction pattern from Beringia east to isolated tundra in eastern North America.

C - subtraction pattern from the Rocky Mountains to the sierra of California.

All species found at the end of each arrow are present at the beginning of the arrow.

16
A
10
B
10
5
C
14
3
12
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

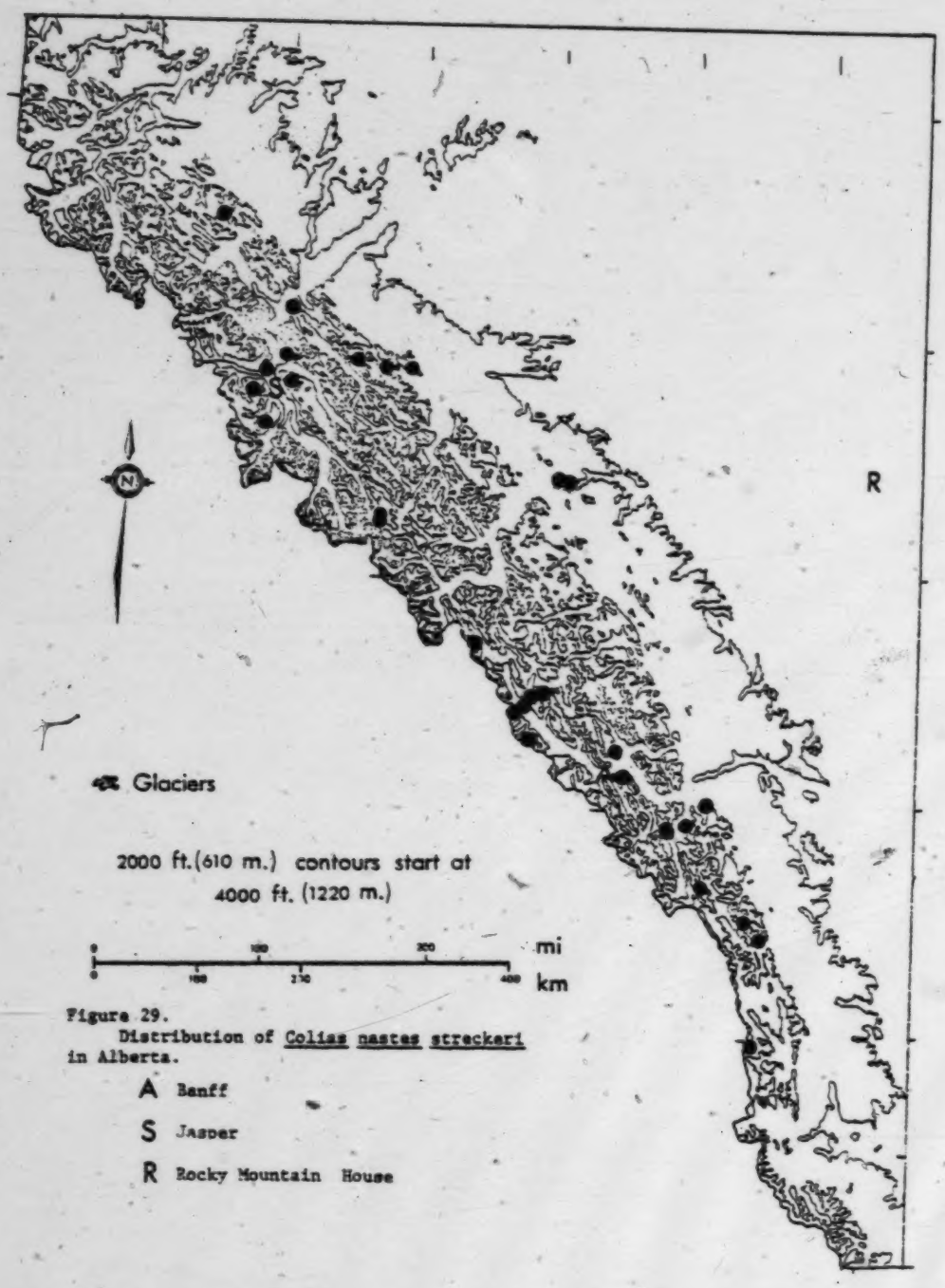


Figure 29.
Distribution of Colias nastes streckeri in Alberta.

A Banff

S Jasper

R Rocky Mountain House

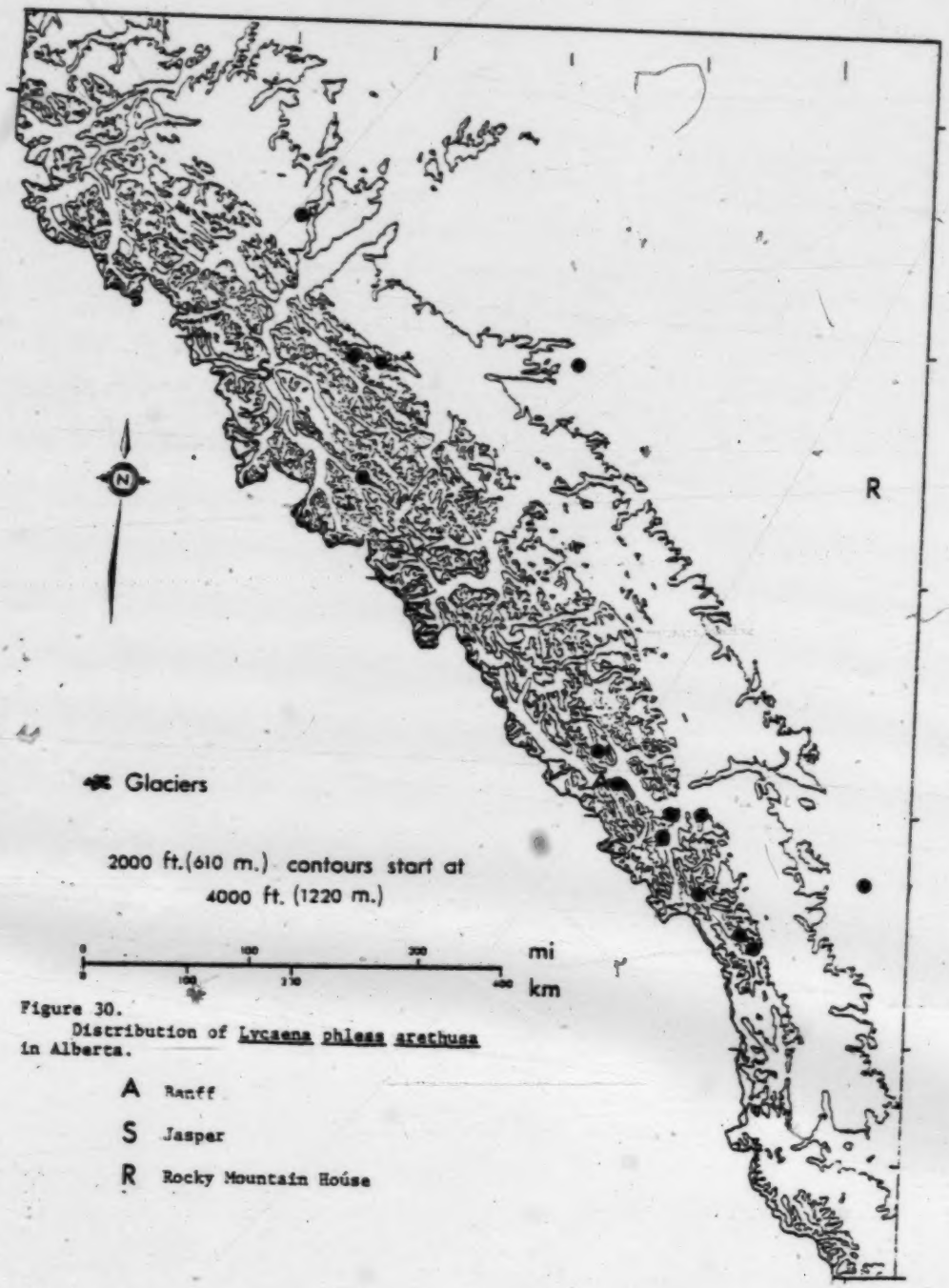


Figure 30.
Distribution of Lycaena phlaas arethusa in Alberta.

A Banff

S Jasper

R Rocky Mountain House

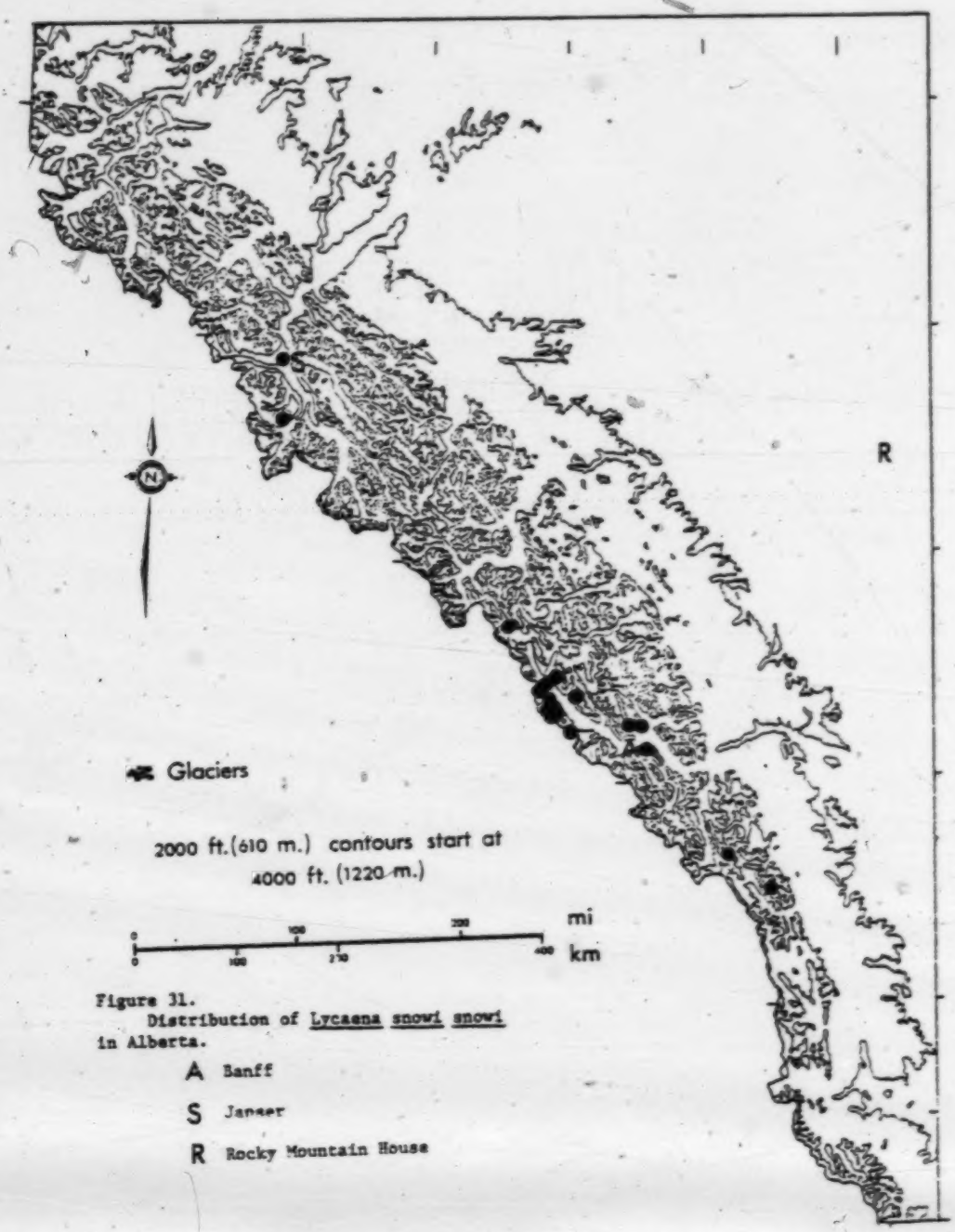


Figure 31.
Distribution of Lycaena snowi snowi in Alberta.

A Banff

S Jasper

R Rocky Mountain House

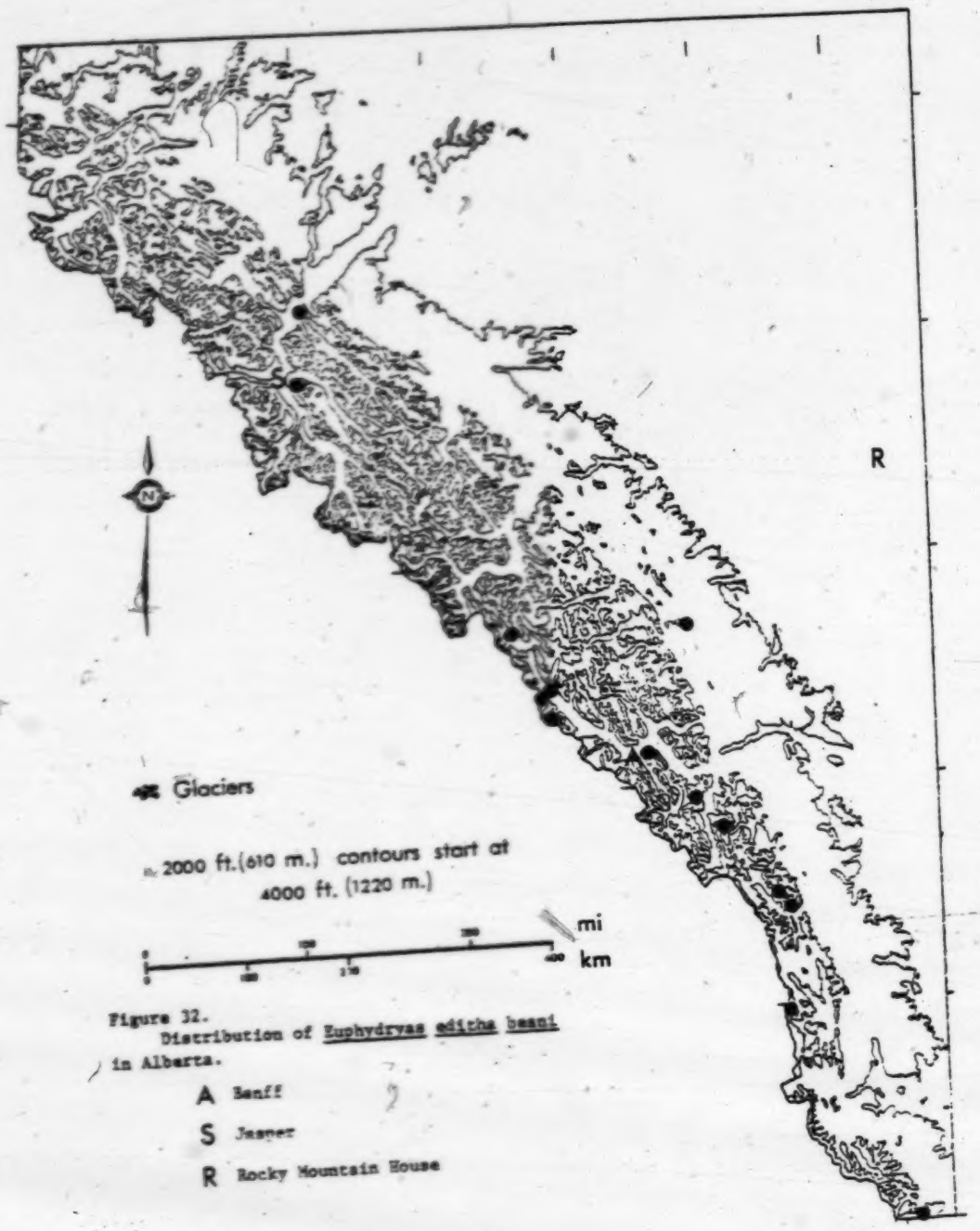


Figure 32.
Distribution of Euphydryas editha beani in Alberta.

A Banff

S Jasper

R Rocky Mountain House

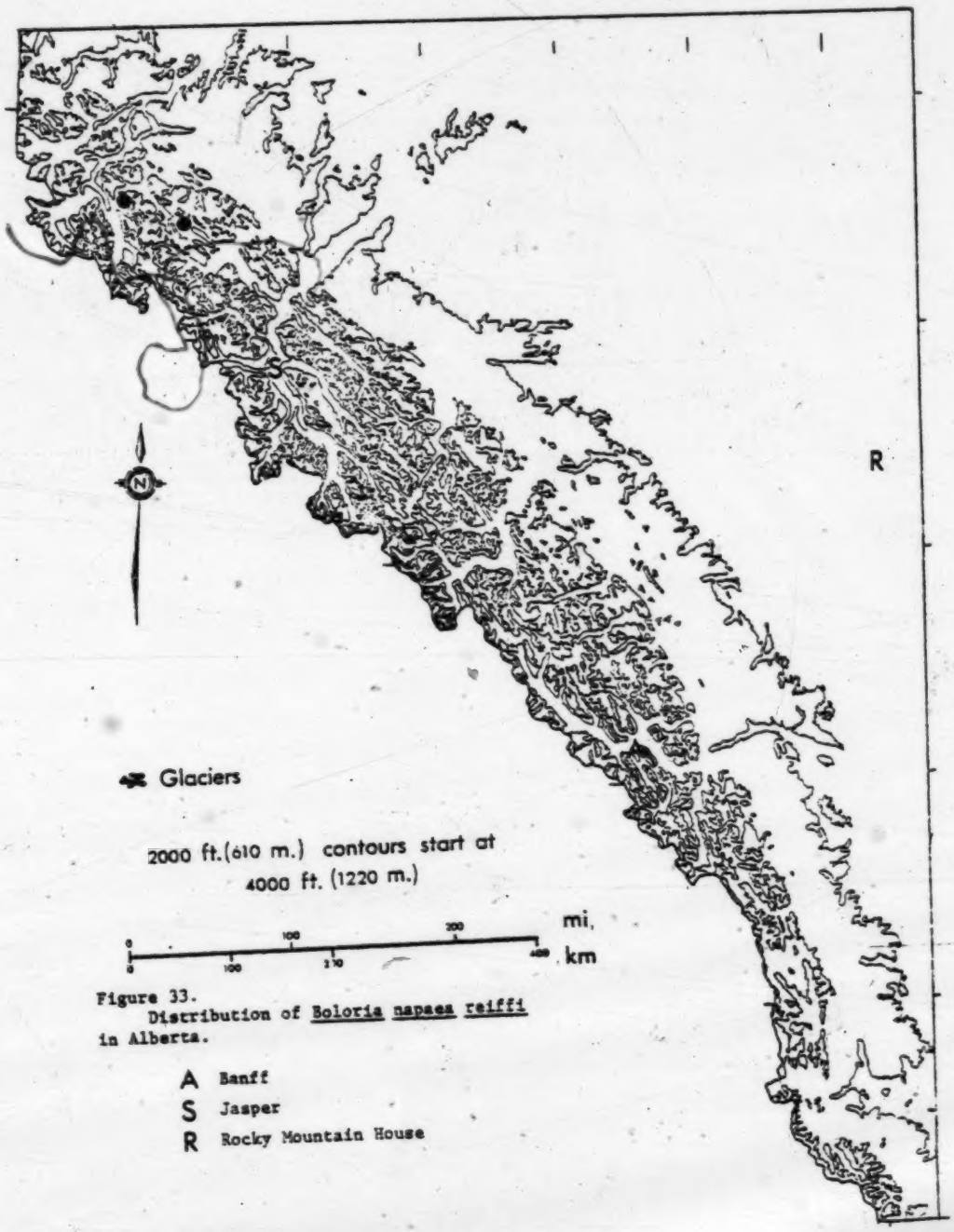


Figure 33.
Distribution of Boloria napaea reiffi in Alberta.

A Banff
S Jasper
R Rocky Mountain House

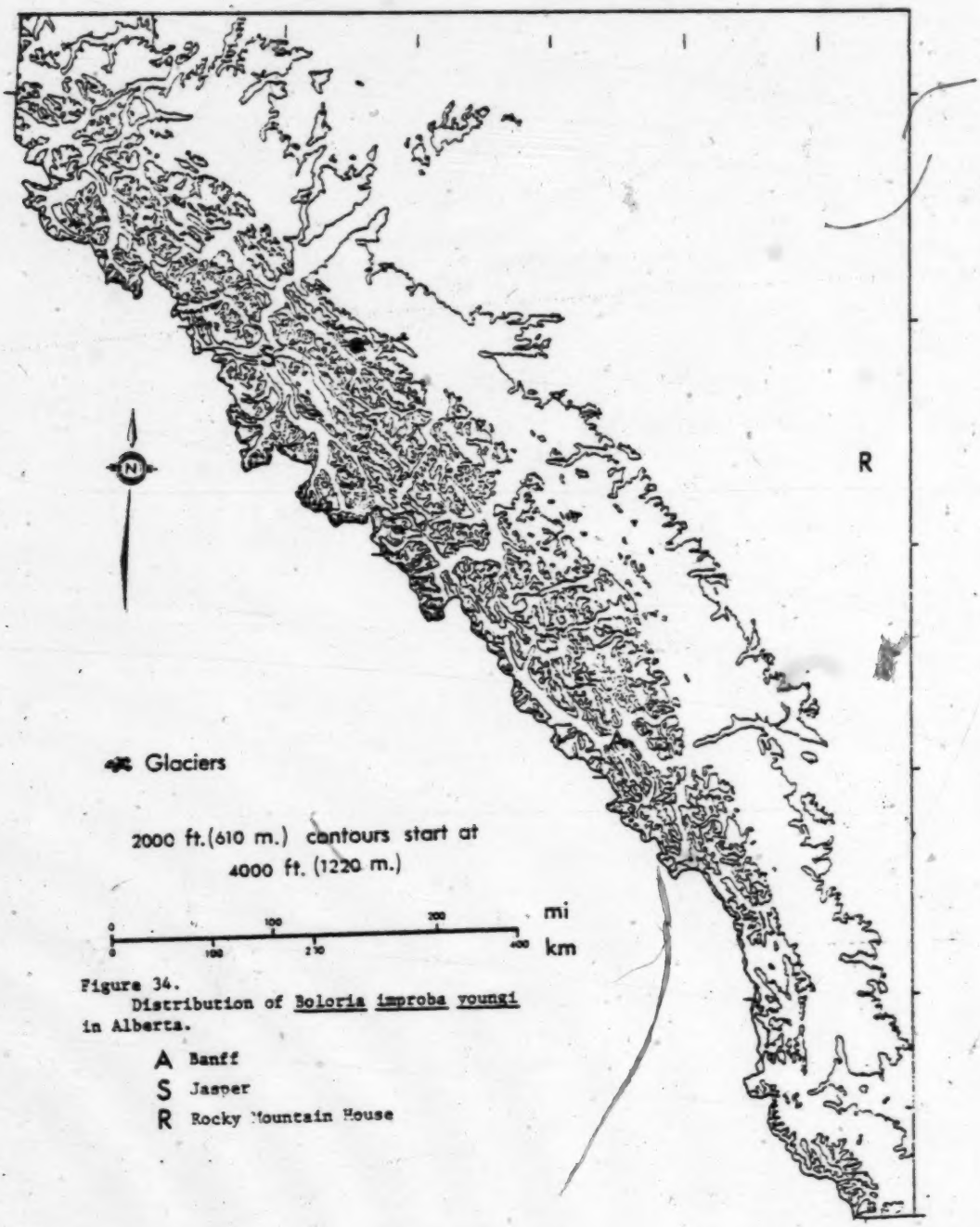


Figure 34.
Distribution of Boloria improba youngi in Alberta.

A Banff
S Jasper
R Rocky Mountain House

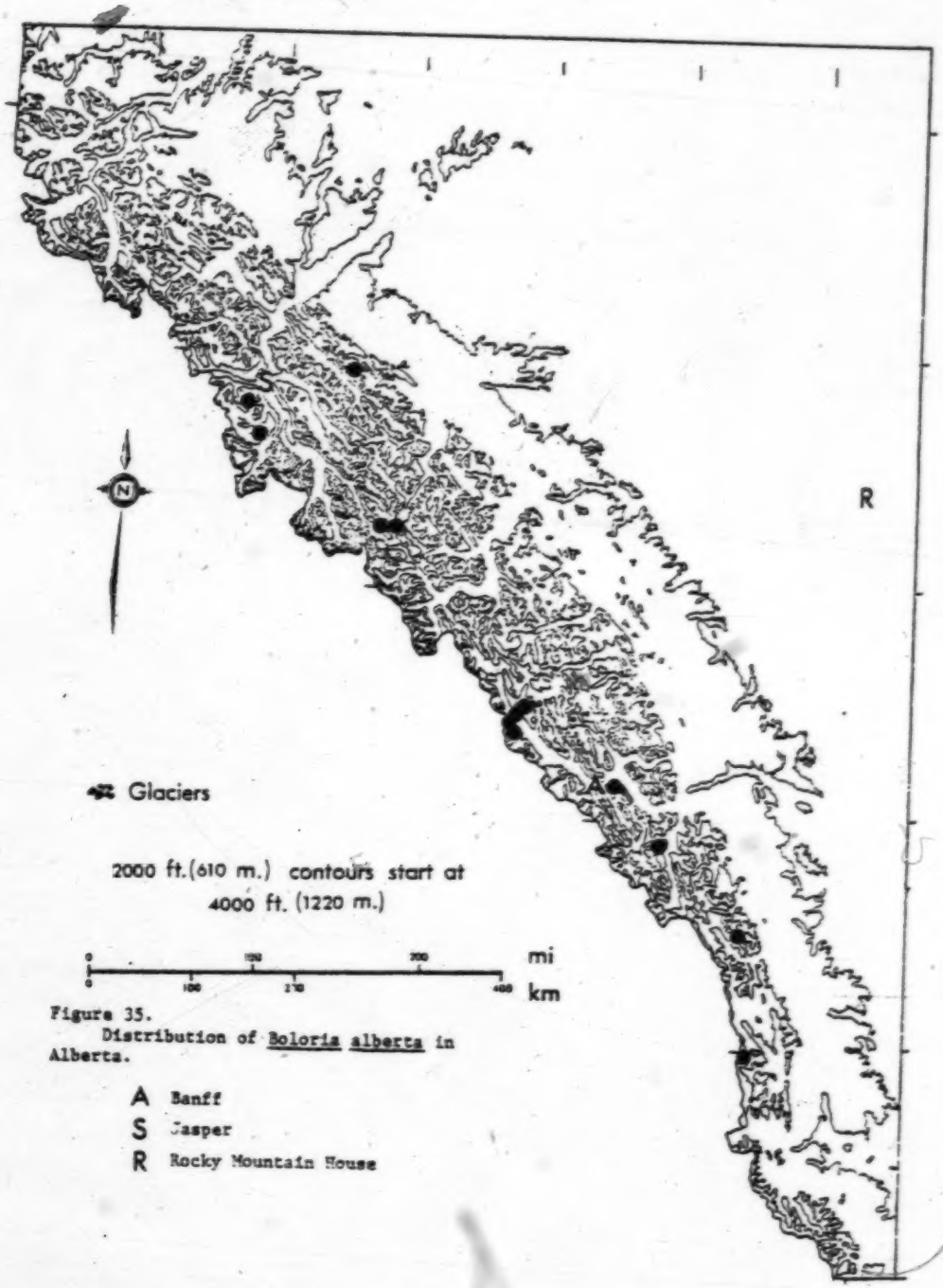


Figure 35.
Distribution of Boloria alberta in Alberta.

A Banff
S Jasper
R Rocky Mountain House

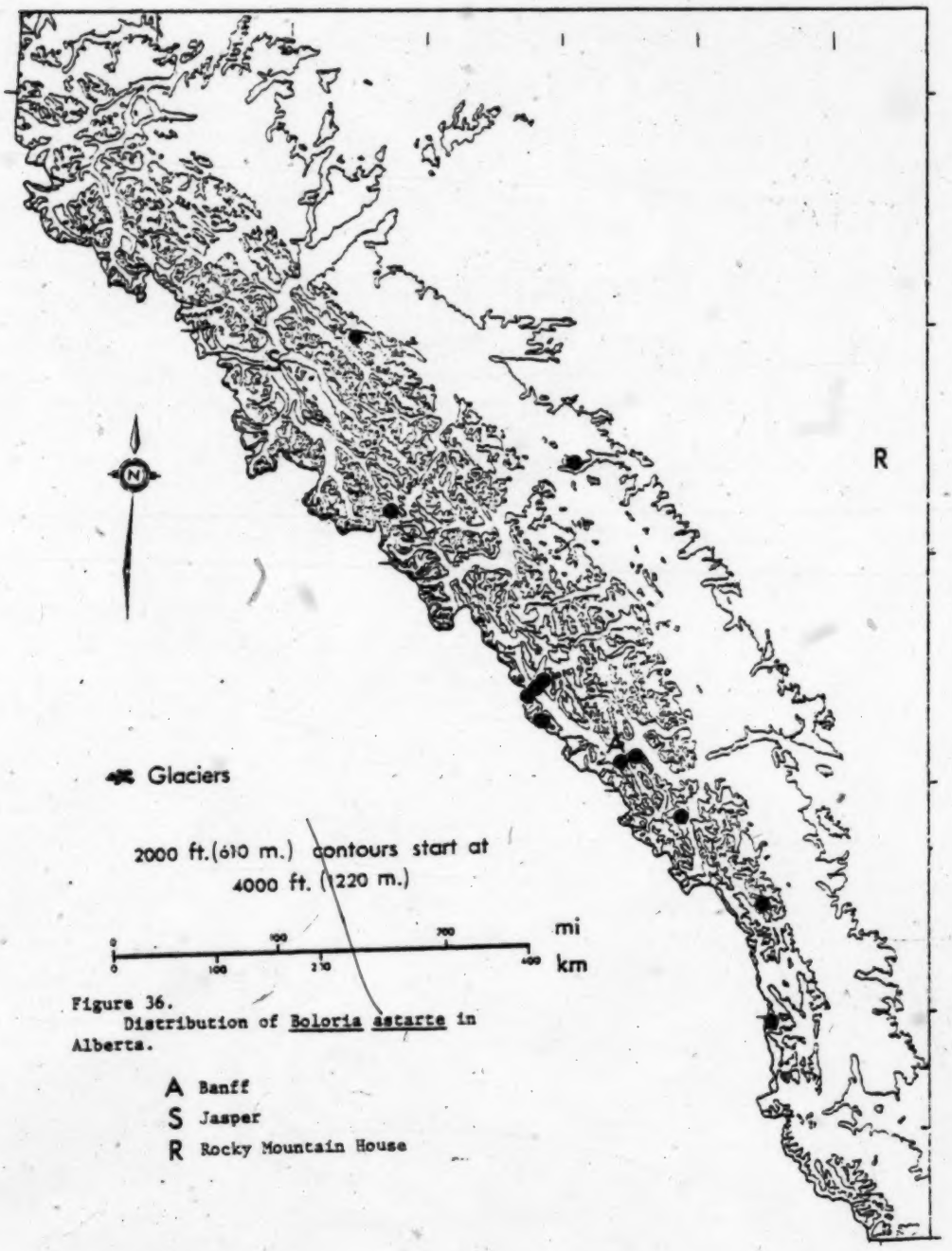


Figure 36.
Distribution of Boloria astarte in Alberta.

A Banff
S Jasper
R Rocky Mountain House

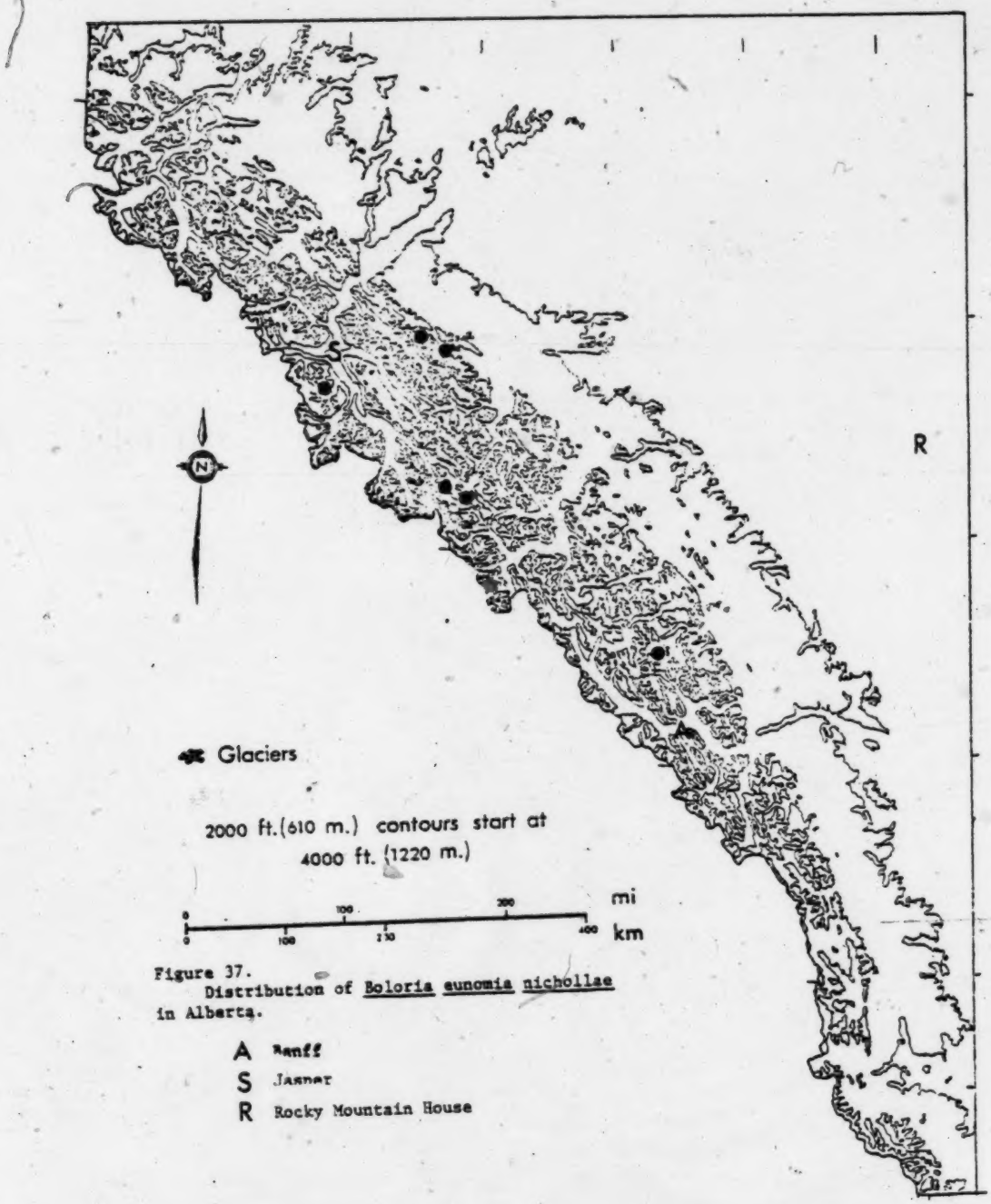


Figure 37.
Distribution of Boloria eunomia nichollae in Alberta.

A Banff
S Jasper
R Rocky Mountain House

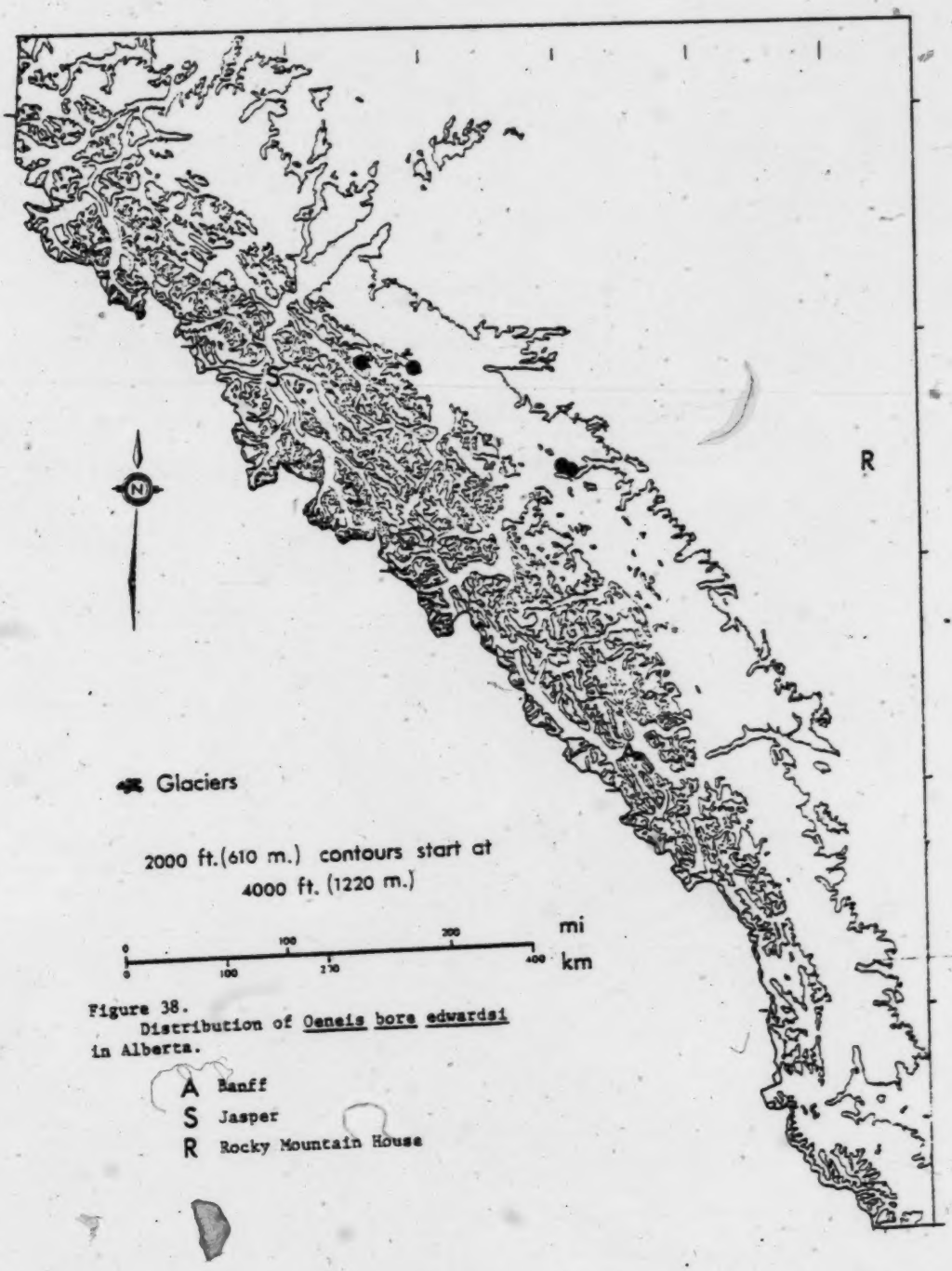


Figure 38.
Distribution of Oeneis bore edwardsi in Alberta.

A Banff
S Jasper
R Rocky Mountain House

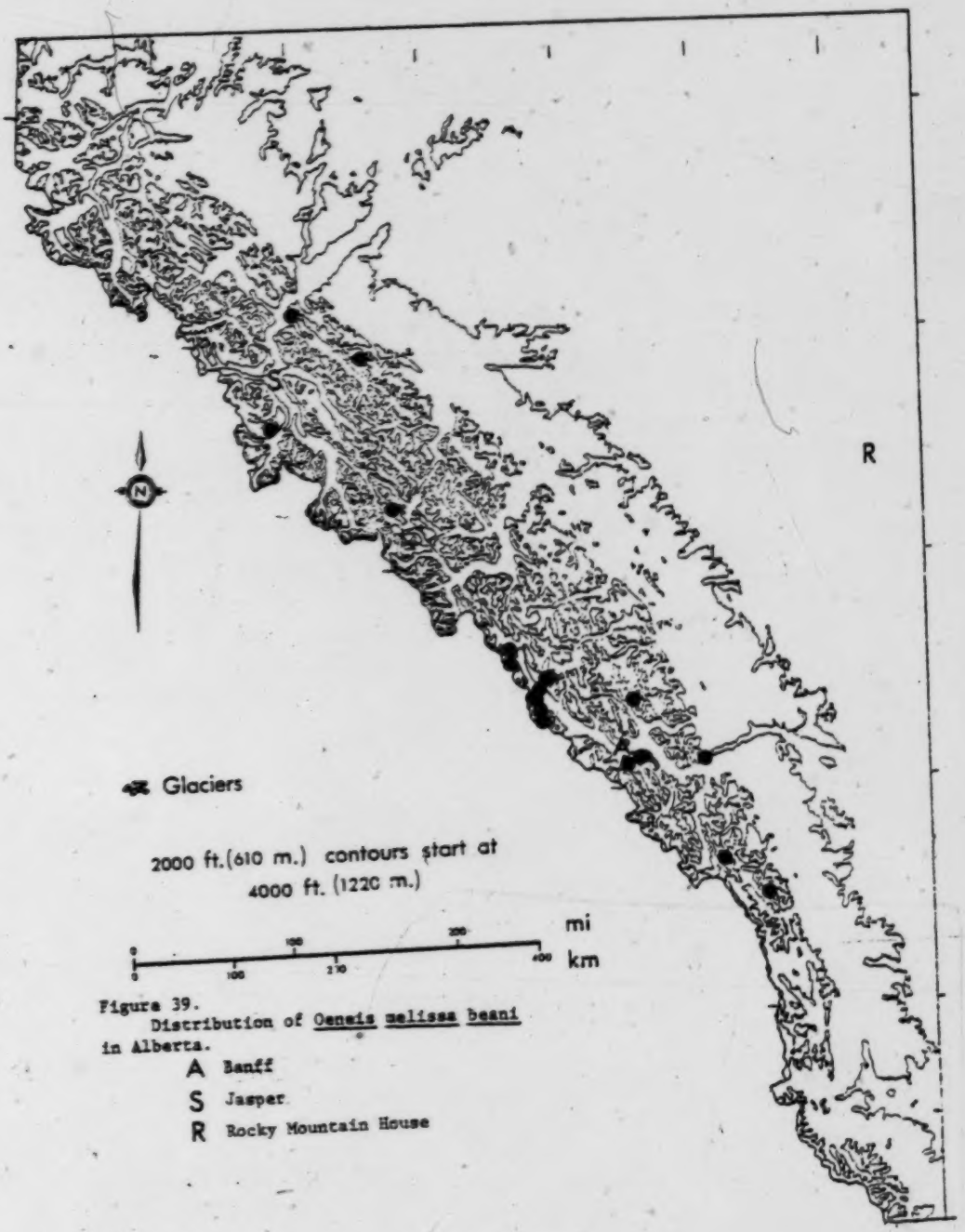


Figure 39.
Distribution of Oeneis melissa beani in Alberta.

A Banff
S Jasper
R Rocky Mountain House

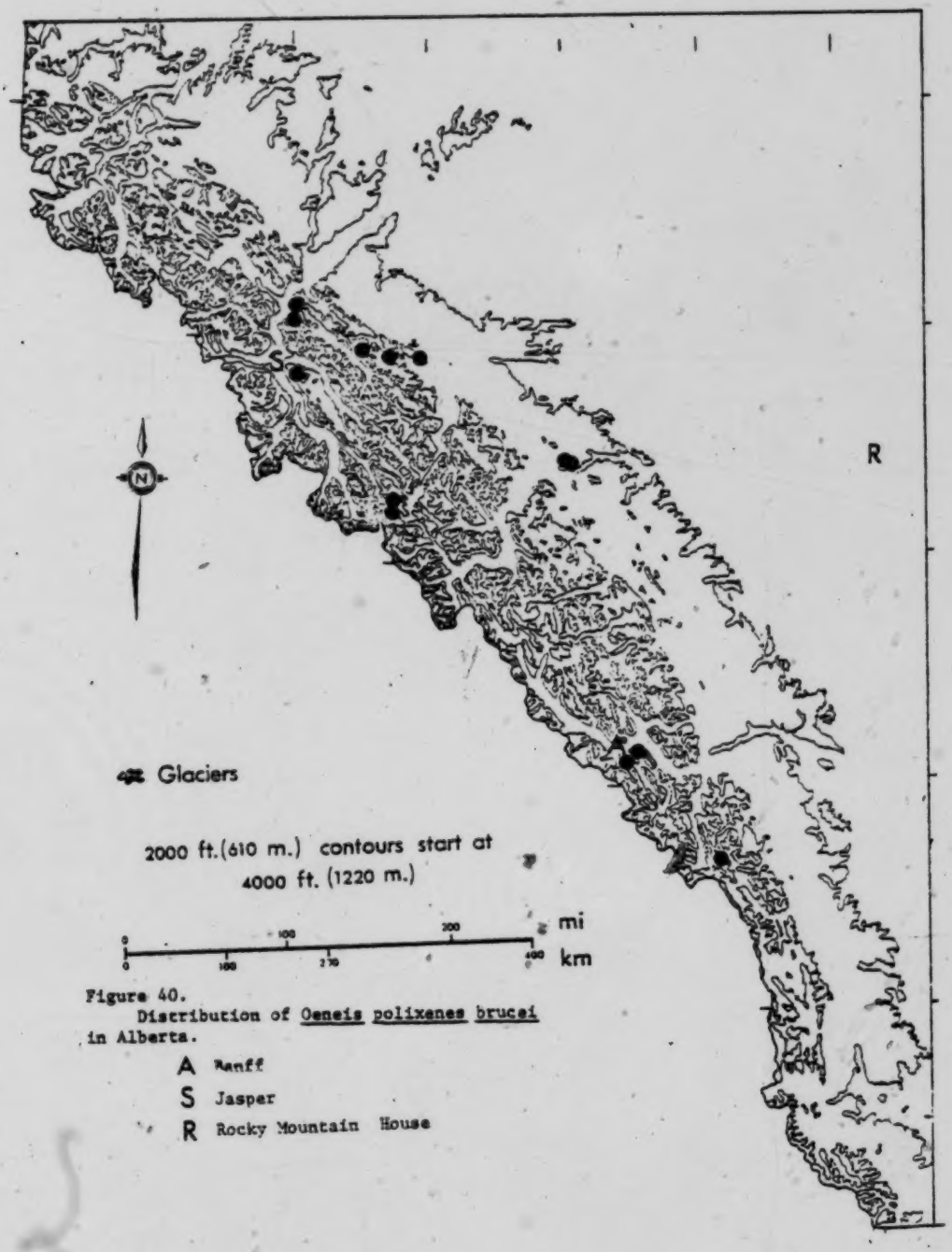


Figure 40.
Discribution of Oeneis polixenes brucei in Alberta.

A Banff
S Jasper
R Rocky Mountain House

Figure 41.

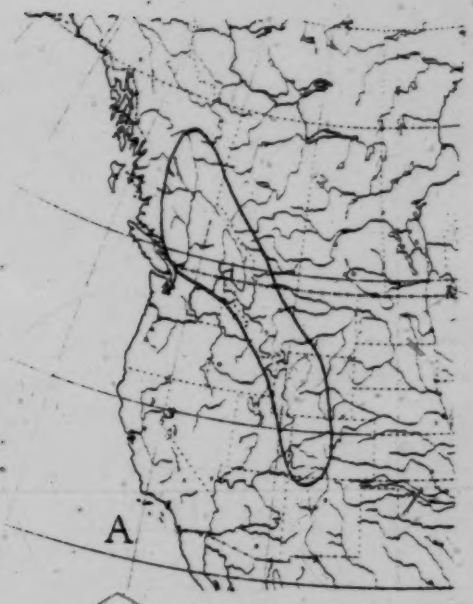
Distribution types exibited by Alberta tundra butterflies.

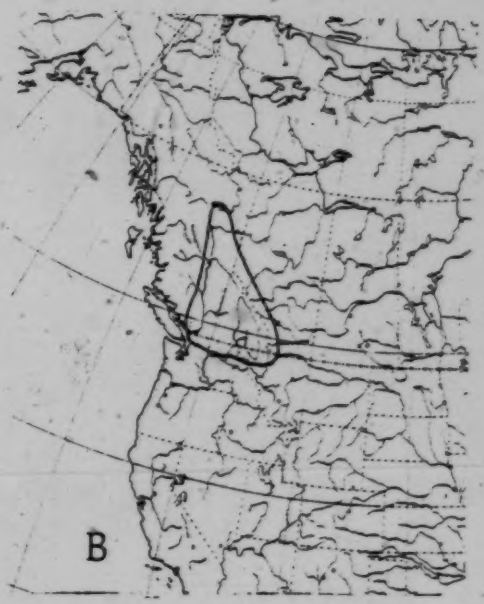
A - Southern Montane.

B - Central Montane.

C - Disjunct populations.

D - Endemic forms.


A


B

C

D

Figure 42.

Extent of Early Wisconsin ice in the Mountain Park area. Vertical hatching indicates the presence of ice. Note extensive unglaciated areas above 6500 feet. Modified from data in Reimchen and Bayrock, 1977. The location of the town of Mountain Park is indicated by dot "A".

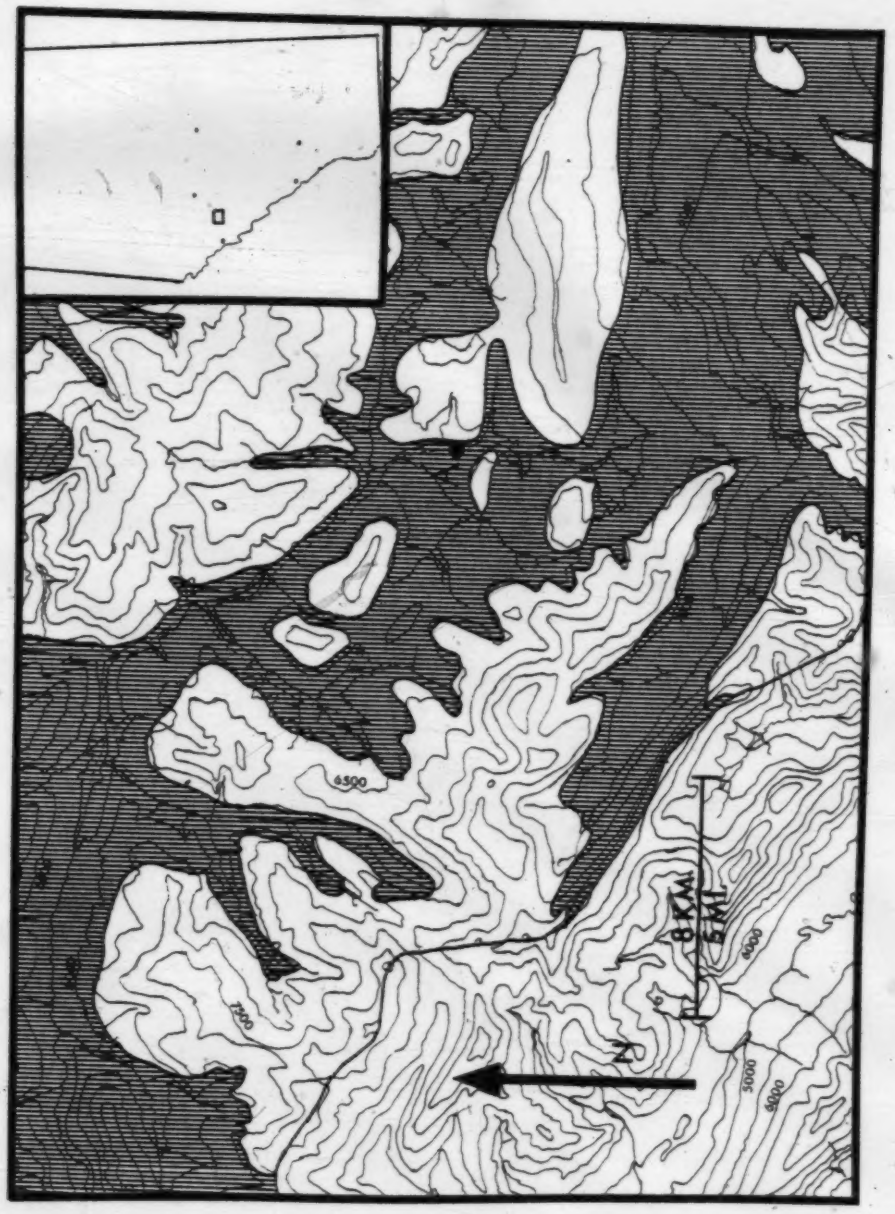

6500
7500
5000
6000
8 KM
5 MI
N

Figure 43.

Retreat of Wisconsin and recent ice sheets in Western Canada modified after Prest (1969).

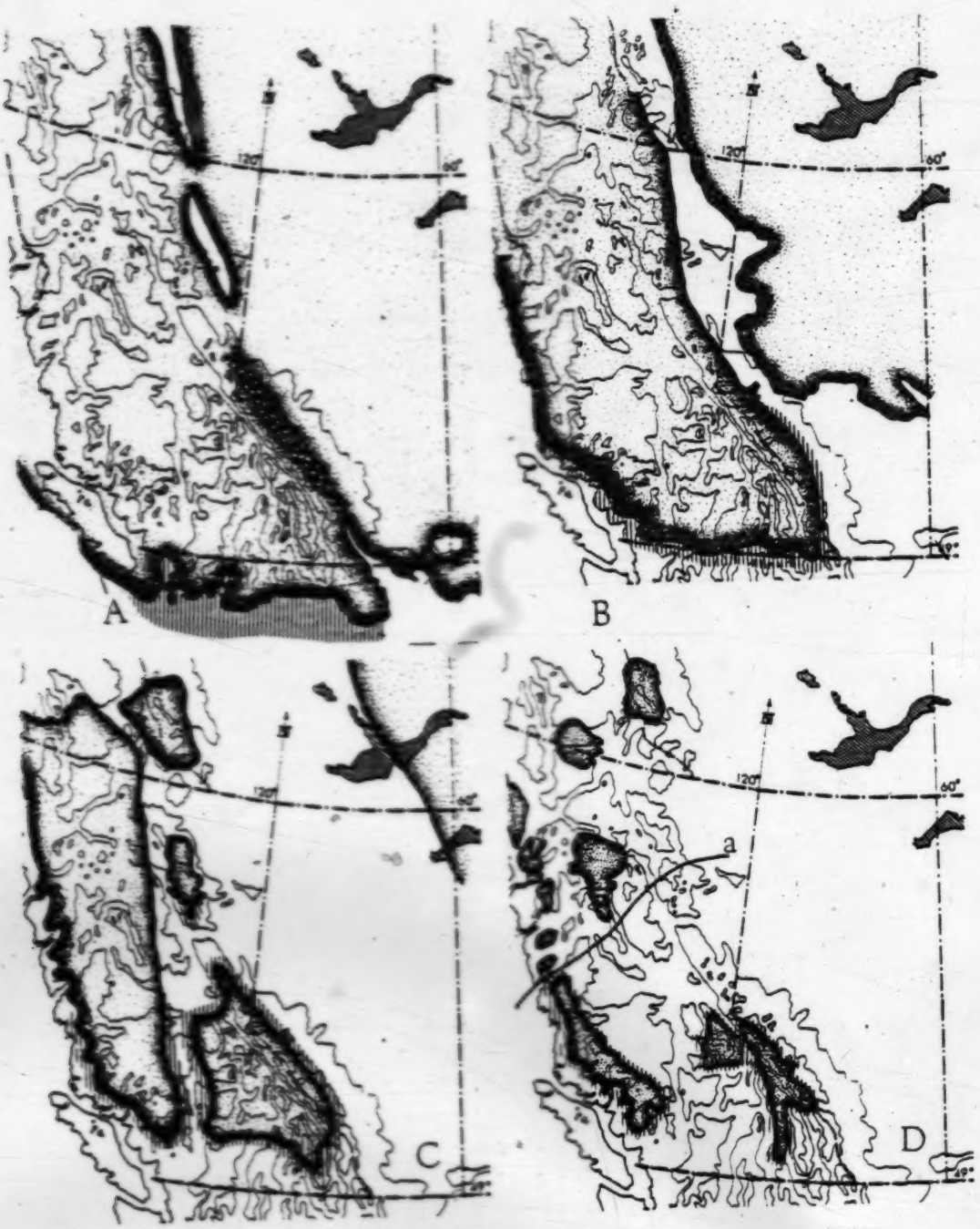
A - 17,000 to 15,000 years before present.

B - 12,000 years before present.

C - 10,000 years before present.

D - 8,000 years before present.

Stipled areas correspond to continental ice sheets. The colonization of Alberta by taxa in the refugium south of the ice sheets is indicated by vertical hatching. In C and D this tundra would be very narrow, perhaps less than 1 kilometer. In D, line 'a' indicates the limit of northern dispersal.


120°
60°
A
B
C
a
D

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APPENDIX 1. LOCALITY DATA

5.1 Parnassius eversmanni thor

CANADA: British Columbia: Atlin; Mount Hoadley, Pink Mountain. Yukon Territory: Dempster Highway, mile 45, mile 52; Keno Hill; Sam Lake.

UNITED STATES: Alaska : Anaktuvuk Pass; Atigun River; Denali Highway, mile 13, mile 14; Eagle Summit; Galbraith Lake; Highway Pass; Itigaknit Mountain; Itkillik River; Kavik River; Kivalina River; Lake Schraeder; Marsh Fork, Canning River; Mount McKinley National Park, Hotel and vicinity; Kantishna; Mount Fairplay; Noatak River Valley; Noluck Lake; Nome and vicinity; Nome-Teller Road, mile 28; Ogotoruk Creek; Oksrukuyik; Sagwon; Sheenjek River; Slime Creek and Nenana River; Steese Highway, mile 90.2, mile 102; Utukok River.

5.2 Colias boothi

CANADA: North West Territories: Arctic Bay; Baillarge Bay; Baker Lake; Banks Island; Bathurst Island; Bernard Harbour; Chesterfield Inlet; Coppermine; Coral Harbour; Coronation Gulf; Cambridge Bay; Eskimo Point; Holman Island; Muskox Lake; Padlei; Pond Inlet; Reindeer Depot; Repulse Bay; Sachs Harbour; Spence Bay; 5 from Freeman (1956). Yukon Territory: Herschel Island; Keno Hill; Sam Lake.

5.3 Colias nastes thula

UNITED STATES: Alaska: Aichilik River; Anaktuvuk Pass; Cape Sabine; Galbaith Lake; Head of Canning River; Healy and vicinity; Hulahula River; Itigaknit Mountain; Itkillik River; Kavik Lake; Kivalina River; Kougarok Road, mile 50; Lake Schraeder; Marsh Fork Canning River; Mount Distin;

Noluck Lake; Nome and vicinity; Nome-Teller Road, mile 18, mile 21, mile 28, mile 42; Ogotoruk Creek; Sadlerochit Springs; Sagwon; Sheenjek River; Toolik Lake; Utukok River.

5.3 Colias nastes

CANADA: Alberta : Bald Hills, Jasper; Banff; Burnt Timber Lookout; Cascade Mountain; Columbia Ice Fields; Divide Pass; Fossil Mountain; Hailstone Butte; Highwood Pass; Jasper; Kanacamp; Laggan (Lake Louise); Moose Mountain; Moraine Lake; Mount Edith Cavell; Mount McBride; Mount St. Piran; Nordegg (Shunda and Coliseum Mountains); Peyto Lake; Plateau Mountain; Pocahontas; Pope-Thoreau Pass; Prospect Mountain; Red Cap Mountain; Signal Mountain; Storm Mountain; Sunwapta Pass; The Fortress (Fortress Mountain); The Whistlers (Whistlers Mountain); Toronado Pass; Whitehorn (Mountain); Wilcox Pass; Willow Creek Pass. British Columbia: Atlin; Creater Mountain; Garibaldi; Lillooet; Mount Ball; Mount Mclean; Panorama Ridge, Garibaldi; Pearson Mountain; Pink Mountain; Vavenby. Newfoundland and Labrador: Hebron. Manitoba: Churchill. North West Territories: Anderson River; Arctic Bay; Baillarge Bay; Baker Lake; Banks Island; Bathurst Inlet; Bernard Harbour; Cambridge Bay; Cockburn Point; Coppermine; Coral Harbour; Eskimo Point; Eureka; Frobisher Bay; Gjoa Haven; Godlin Lakes; Holman Island; Hutchinson Bay; Kuujua River; Muskox Lake; Pond Inlet; Reindeer Depot; Repulse Bay; Sachs Harbour; Saw Mill Bay; Spence Bay. Quebec : Fort Chimo; Payne Bay; Port Harrison; Sugluk. Yukon Territory: Burwash Landing; Herschel Island; 16 from Freeman (1956).

UNITED STATES: Alaska: Anaktuvuk Pass; Barter Island; Beaufort Lagoon; Black Rapids; Cape Epsburg; Collinson Point; Eagle Summit; Galbraith Lake;

Head of Canning River; Hulahula River; Kiguaik Mountains; Kivalina River; Kougarok Road, mile 50; Lake Schraeder; Marsh Fork Canning River; Mount Distin; Mount Fairplay; Mount McKinley National Park, Kantishna; Noatak River Valley; Noluck Lake; Nome and vicinity; Nome-Teller Road, mile 18, mile 21; Ogotoruk Creek; Okpilak River; Rustic Village; Sagwon; Sheenjek River; Toolik Lake; Twelve Mile Summit; Utukok River. Washington: Slate Peak, Okanagan county. Montana: Flathead County; Glacier County.

5.4 Lycaena phleas

CANADA: Alberta: Banff; Burnt Timber Lookout; Brazeau Creek; Elk River area; Grande Cache; Hailstone Butte; Highwood Pass; Moberly Creek; Moose Mountain; Mountain Park; Pidgeon Mountain; Plateau Mountain; Poboktan Creek; Prospect Mountain; Sheep River, 30 miles south west of Calgary; Snow Ridge (The Fortress); Vermillion Range. British Columbia: Mount Goldbridge(?). North West Territories: [illegible]ic Bay; Baker Lake; Bathurst Inlet; Bernard Harbour; Cockburn Point; Coppermine; Eureka; Frobisher Bay; Gjoa Haven; Holman Island; Pond Inlet; Repulse Bay. Yukon Territory: Burwash Landing; Klotassin River; Kluane Lake; Tindir Creek.

UNITED STATES: Alaska: Highway Pass; Lake Schraeder; Mount McKinley National Park, Kantishna; Noluck Lake; Ogotoruk Creek; Okpilak River; Rustic Village. Montana: Flathead County; Glacier County.

14 from Butterflies of the southern Rocky Mountains.

4 from Freeman (1956).

5.5 Lycaena snowi

CANADA: Alberta: Banff; Bow Pass; Cascade Mountain; Consolation Lakes; Goat Lake; Highwood Pass; Jasper; Laggan (Lake Louise); Morain Lake; Mount Edith Cavell; Mount Fairview; Mount St. Piran; Whitehorn; Paradise (valley?); Plateau Mountain; Valley of the Ten Peaks; Vermillion Range. British Columbia: Bear Lake; Boom Pass; Garibaldi; Lillooet; Mount McLean; Panorama Ridge, Garibaldi.

UNITED STATES: 47 from "Butterflies of the southern Rocky Mountains".

5.6 Euphydryas editha

CANADA: Alberta: Bald Hills; Banff; Bow summit (pass); Burnt Timber Lookout; Crypt Lake; Goat Lake; Hailstone Butte; Highwood Pass; Lake Louise; Mount McBride; Mount St. Piran; Panther River; Paradise Valley; Plateau Mountain; Pocahontas; The Fortress (Fortress Mountain); Tornado Pass. British Columbia: Cathedral Lakes; Manning Provincial Park; Mount Kobau.

UNITED STATES: Oregon: Mount Hood; Mount Theilsen, Douglas County.

5.7 Boloria napaea

CANADA: Alberta: Headwaters of the Berland River; Kvass Creek Summit (near Kvass Creek Fire Lookout). British Columbia: Monarch Mountain, Atlin; Pink Mountain; Red Fern Lake; Summit Lake. North West Territories: Anderson River; Atkinson Point; Baker Lake; Bathurst Inlet; Bernard Harbour; Coppermine; Holman Island; Minto Inlet; Thelon River; Tununuk Point. Yukon Territory: Haines Junction; Herschell Island; Keno

Hill; Kluane Lake; Old Crow; Raquet Creek; Whitehorse.

UNITED STATES: Alaska: Aichilik River; Anaktuvuk Pass; Black Rapids; Chugach Mountains; Old Creek trail, north of Girdwood; Denali Highway, mile 11-13, mile 14; Eagle Summit; Galbraith Lake; Hatcher Pass; Head of Canning River; Hope; Imuruk Lake; Kavik River; Kivalina River; Kodiak Island; Uganik Lake; Kougarok Road, mile 50; Kugluaik Mountains; Lake Schraeder; Lazy Mountain, Red Mountain; Marsh Fork Canning River; Mount McKinley National Park, Kantishna; Mount Distin; Naotak River; Noluck Lake; Nome and vicinity; Nome-Teller Road, mile 18, mile 21 mile 28, mile 42; Ogotoruk Creek; Okpilak River; Partan Mountains, Chilcat Pass; Rustic Village; Sagavinirktok River; Sagwon; Sheenjek River; Tangle Lakes; Thorofare Pass; Twelve mile summit; Utukok River. Wyoming: Green River Pass, Sublette County.

4 from Freeman (1956).

5.8 Boloria improba

CANADA: Alberta: Prospect Mountain. British Columbia: Monarch Mountain, Atlin; Pink Mountain; Red Fern Lake; Summit Lake. North West Territories: Atkinson Point; Baker Lake; Banks Island; Bernard Harbour; Cape Parry; Chesterfield; Coppermine; Eskimo Point; Frobisher Bay; Holman Island; MacKay Lake; Minto Inlet; Muskox River; Padlei; Port Epworth; Repulse Bay; Sachs Harbour; Spence Bay. Yukon Territory: Bear Creek Pass; Burwash Landing; Hains Junction; Herschell Island; Keno Hill; Kluane Lake; Sam Lake.

UNITED STATES: Alaska: Aichilik River; Anaktuvuk Pass; Barter Island; Beaufort Lagoon; Cape Sabine; Eagle Summit; Head of Canning River; Highway

Pass; Hulahula River; Itigaknit Mountain; Kavik River; Kivalina River; Konganevuk; Lake Schraeder; Mount Fairplay; Noatak River Valley; Noluck Lake; Nome and vicinity; Nome-Teller Road, mile 18, mile 21, mile 42; Ogotoruk Creek; Okpilak River; Sagwon; Sheenjek River ; Utukok River. 7 from Freeman, (1956).

5.9 Boloria polaris

CANADA: British Columbia: Pink Mountain; Summit Lake (mile 391, Alaska Military Highway). Manitoba: Churchill. Quebec: Cape Chidley; Fort Chimo; Knob Lake; Port Harrison. North West Territories: Alert; Armstrong Point; Baker Lake; Banks Island; Bathurst Inlet; Bernard Harbour; Cambridge Bay; Cape Krusenstern; Cape Parry; Cape Ross; Chesterfield Inlet; Chick Lake; Coppermine; Coral Harbour; Eskimo Point; Eureka; Frobisher Bay; Holman Island; Hutchinson Bay; Inuvik; Kalil-took-duag (Quebec?); Lake Angmaloktak, Colville Mountains; MacKay Lake; Melville Island; Padlei; Port Epworth; Reindeer Depot; Repulse Bay; Sachs Harbour; Saw Mill Bay; Spense Bay; Truelove lowland; Tununuk Point; Walker Bay; Wallaston Land. Yukon Territory: Dempster Highway, mile 45.5, mile 82, mile 87; Nines Creek; Rampart House.

UNITED STATES: Alaska: Anaktuvuk Pass; Barter Island; Beaufort Lagoon; Denali Highway, mile 14; Eagle Summit; Hulahula River; Itkillik River; Itigaknit Mountain; Kavik River; Kivalina River; Kongakut River; Lake Schraeder; Marsh Fork Canning River; Mount Distin; Murphy Dome; Nahtuk Creek, Alatna River; Noatak River; Noluck Lake; Nome and vicinity; Nome-Teller Road, mile 18; Ogotoruk Creek; Olpilak River; Sagwon; Sheenjek

River; Slime Creek at Nenana River; Utukok River.

DENMARK: Greenland: Qanaq.

11 from Freeman (1956).

5.10 Boloria alberta

CANADA: Alberta: Banff; Headwaters of the Saskatchewan and Athabasca Rivers; Laggan (Lake Louise); Lake Ohara; Mount Edith Cavell; Mount Fairview; Mount St. Piran; Mount Whitehorn; Nigel Pass; Parker Ridge; Plateau Mountain; Prospect Mountain; The Fortress (Fortress Mountain); The Whistlers (Whistlers Mountain); Tornado Pass; Wilcox Pass British Columbia Boulder Pass; Ptarmigan Lake (?); Lillooet; Mount Assiniboine; Mount Hector; Snow Creek Pass (?): Yoho Valley.

UNITED STATES: Alaska: Anaktuvuk Pass. Montana: Going to Sun Mountain Glacier County; Grinnel Point, Glacier County; Mount Reynolds, Glacier County.

5.11 Boloria astarte

CANADA: Alberta: Banff; Burnt Timber Lookout; Coliseum Mountain; Headwaters of the Saskatchewan and Athabasca Rivers; Laggan (Lake Louise); Lake Ohara; Moraine Lake; Mount St. Piran; Mount Whitehorn; Plateau Mountain; Prospect Mountain; Snow Creek Pass; Sulfer Mountain; The Fortress (Fortress Mountain); Tornado Pass; Wapta Lake. British Columbia: Eagle Mountain (?); Emerald Lake; Mount Cheam; Pink Mountain.

UNITED STATES: Montana: Glacier Crest, Flathead County; Glacier National Park, Glacier County. Washington: Cooney Mountain; Haystack Mountain; Slate Peak, Okanagan County.

5.12 [illegible]oria distincta

CANADA: British Columbia: Atlin. North West Territories: Eduni Mountain, Gravel River; 200 miles south of the arctic ocean on Yukon Territory border. Yukon Territory: Dempster Highway, mile 97; Harrington Creek; Keno Hill; Kluane Lake; Sam Lake; Tindir Creek.

UNITED STATES: Alaska: Crow Creek Trail, north of Girdwood; Eagle Summit; Hulahula River; Itigaknit Mountain; Kathul Mountain; Kivalina River; Lava Lake; Mount Distin; Noluck Lake; Nome and vicinity; Nome-Teller Road, mile 18, mile 21, mile 42; Utukok River.

5.13 Boloria eunomia

CANADA: Alberta: Divide Pass; Mount Edith Cavell; Nigel Pass; Prospect Mountain; Snow Creek Pass; Wilcox Pass.

UNITED STATES: Colorado: Hall Valley, Park County. Montana: Carbon County. Wyoming: Beartooth Plateau, Park County; Big Horn County; Lewis Lake, Albany County.

13 from Butterflies of the southern Rocky Mountains

5.14 Oeneis bore

CANADA: Alberta: Nordegg, Baldy Lookout (Shunda Mountain); Nordegg, Coliseum Mountain; Prospect Mountain; Red Cap Mountain. British Columbia: Pink Mountain; Red Fern Lake. Manitoba: Churchill. Newfoundland and Labrador: Happy Valley, Goose Bay; Hebron; Hopedale; Nain; Nastpoka River; Rama; Rupert House. North West Territories: Anderson River; Atkinson Point; Baker Lake; Bathurst Inlet; Cape Krusenstern; Colden Lake; Coppermine; Coronation

Gulf; Grays Bay; Holman Island; Hutchinson Bay; Inuvic; Kidluit Bay; King George Sound; Muskox Lake; Padlei; Reindeer Depot; Tununuk Point; Whale River. Quebec: Belcher Islands; Fort Chimo; Great Whale River; Little Cape Jones; Mount Albert; Payne Bay; Port Burwell; Port Harrison; Suglug; Wolsenholme. Yukon Territory: Alaska Military Highway, mile 1167; Bear Creek Pass; Burwash Landing; Carcross; Dempster Highway, mile 45.5, mile 82, mile 135; Haines Highway, mile 101; Kathleen Lake; Kluane Lake; Kluane Road, Marshall Creek; Nation River; Old Crow; Rampart House; Shoalwater Bay; Sitdown Creek; Siwash Creek; Spencer Creek and Alaska Military Highway; West of Swift River on Alaska Military Highway; Whitehorse.

UNITED STATES: Alaska: Aichilik River; Alfred Creek Camp (unspecified); Anaktuvuk Pass; Atigun River; Big Lake (22 miles W.N.W. wiseman); Birch Creek (mile 137 Steese Highway); Boulder Creek (unspecified); Delta Junction; Denali Highway, mile 11-13, mile 14, mile 35, mile 34-40, mile 77, mile 125; Eagle Summit; Fort Yukon; Galbraith Lake; Gulkana River; Head of Canning River; Healy; Hope; Hulahula River; Iliamna River; Imuruk Lake; Itigaknit Mountain; Kandik River; Kavik River; Kivalina River; Kongakut River; Kuskoquim River; Lake Schraeder; Lava Lake; Marsh Fork Canning River; Mount McKinley National Park; Mount McKinley National Park, Kantishna; Mentasta Mountains; Mount McKinley; Nahtuk Creek; Noatak River Valley; Noluck Lake; Nome-Teller Road, mile 28, mile 42; Oksrukuyik (Sagavanirktok River); Rustic Village; Sagavanirktok River; Sagwon; Saint Michaels; Sheenjek River; Sheep Mountain; Shishmaref; Slime Creek at Nenana River; Steese Highway, mile 90, mile 90.2, mile 97.2, mile 102; Teller; Toolik Lake; Umiat; Utukok River; Willow Bay. Colorado: San Juan Mountains,

Hinsdale County.

9 from Butterflies of the southern Rocky Mountains.

13 from Freeman (1956).

5.15 Oeneis melissa

CANADA: Alberta: Agnes Lake; Banff; Banff, 13 miles north; Hector Lake; Highwood Pass; Laggan (Lake Louise); Moraine Lake; Mount Edith Cavell; Mount Fairview; Mount McBride; Mount St. Piran; Mount Whitehorn; Plateau Mountain; Pocahontas; Prospect Mountain; Ptarmigan Mountain; Seebe; Sulfer Mountain; Wilcox Pass; Twp. 36, Rge. 14, W5. Slate Mountain(?). British Columbia: Big Bar; Black Tusk Glacier; Garibaldi; Haystack Mountain(?); Jesmond; Lillooet; Mount Bowman; Mount Cheam; Mount Fields; Mount Luxon; Mount Stevens; Panorama Ridge; Pink Mountain; Windermere, 10 miles east. Manitoba: Churchill Newfoundland and Labrador: no specific localities. North West Territories: Baker Lake; Bernard Harbour; Cambridge Bay; Chesterfield Inlet; Chick Lake; Coral Harbour; Eduni Mountain, Gravel River; Eskimo Point; Fort Reliance; Frobisher Bay; Gravel River and Natla River; Holman Island; Norman Wells; Repulse Bay; Sachs Harbour; Saw Mill Bay; Tununuk Point; Wallaston Land. Quebec: Fort Chimo; Great Whale River; Knob Lake; Mount Jaques Cartier; Port Harrison. Yukon Territory: Dempster Highway, mile 42, mile 82, mile 87; Firth River; Hoole Canyon; Kluane Lake; Nadleen River; Orange Creek; Upper Pelly River; Wolf Canyon.

UNITED STATES: Alaska: Beaufort Lagoon; Eagle Summit; Hope; Ikiakpuk Valley; Itigaknit Mountain; Kivalina River; Kongakut River; Kuskoquim River Valley; Lake Schraeder; Mount Fairplay; Mount McKinley National Park,

Kantishna; Noatak River Valley; Noluck Lake; Nome-Teller Road, mile 21; Ogotoruk Creek; Okpilak River; Rustic Village; Sagavanirktok River; Sagwon; Utukok River; Willow Bay. Washington: Slate Peak, Okanagan County.

30 from Butterflies of the southern Rocky Mountains.

10 from Freeman (1956).

5.16 Oeneis polixenes

CANADA: Alberta: Bald Hills; Banff; Divide Pass; Fort Vermillion (?); Highwood Pass; Nordegg, Mount Shunda, Coliseum Mountain; Pocahontas; Prospect Mountain; Ptarmigan Valley; Red Cap Mountain; Roche Meitte; Sheep Mountain; Sulfer Mountain; Sunwapta Pass; Wilcox Pass. British Columbia: Alaska Military Highway, mile 391; Pink Mountain. Manitoba: Churchill. Newfoundland and Labrador: Hebron. North West Territories: Baillarge Bay; Baker Lake; Boothia Peninsula; Bathurst Inlet; Bernard Harbour; Cambridge Bay; Chantry Island; Chesterfield Inlet; Chick Lake; Coppermine; Eskimo Point; Fort Reliance; Fort Smith; Frobisher Bay; Holman Island; Kidluit Bay; Muskox Lake; Norman Wells; Padlei; Pond Inlet; Reindeer Depot; Repulse Bay; Sachs Harbour; Saw Mill Bay. Quebec: Fort Chimo; Payne Bay; Port Harrison; Sugluk. Yukon Territory: Bear Creek Pass; Burwash Landing; Dempster Highway, mile 52; Firth River at Sheep Creek; Klutlan Glacier.

UNITED STATES: Alaska: Barter Island; Beaufort Lagoon; Cape Pierce; Chugach State Park; Denali Highway, mile 14; Eagle Summit; Highway Pass; Itigaknit Mountain; Itkillik River; Kavik River; Killik River; Kivalina River; Kongakut River; Lake Schraeder; Mount McKinley National Park, Kantishna; Noatak River Valley; Noluck Lake; Nome and vicinity; Nome-Teller

Road, mile 28; Ogotoruk Creek; Okpilak River; Rustic Village; Sagwon; Sheenjek River; Shishmaref; Stampede Road and Toklat River; Steese Highway, mile 90.2; Susitna River; Utukok River; Willow Bay.
8 from butterflies of the southern Rocky Mountains.
18 from Freeman (1956).

5.17 Erebia magdalena

CANADA: Yukon Territory: Dempster Highway, mile 82, mile 97; Firth River at Sheep Creek; Godlin Lakes; Nation River; Rackla River, 12 miles up; Sam Lake.

UNITED STATES: Alaska: Alaska Range, south of Tanacross; Eagle Summit; Head of Canning River; Ikiakpuk Valley; Crow Creek Trail, north of Girdwood; Lake Schraeder; Ogotoruk Creek; Sable Pass, Mount McKinley National Park.
25 from Butterflies of the southern Rocky Mountains.

5.18 Erebia fasciata

CANADA: North West Territories: Armstrong Point; Baker Lake; Banks Island; Bathurst Inlet; Bernard Harbour; Cape Krusenstern; Chesterfield Inlet; Coppermine; Eskimo Point; Godlin Lakes, MacKenzie Mountains; Holman Island; Muskox Lake; Norman Wells; Padlei; Reindeer Depot; Sachs Harbour; Tununuk Point; Walker Bay. Yukon Territory: Bear Creek Pass; Dempster Highway, mile 45; mile 51, mile 82; Firth River at Sheep Creek; Herschell Island; Kluane Lake; Nines Creek; 66° and Boundary; 65° 10' and 141°.

UNITED STATES: Alaska: Aichilik River; Alaska Range, south west of Tanacross; Anaktuvuk Pass; Atigun River; Beaufort Lagoon; Big Lake, 22

miles w. n. w. of Wiseman; Denali Highway, mile 14 ;Eagle Summit; Galbraith Lake; Head of Canning River; Highway Pass; Hulahula River; Imaruk Lake; Itigaknit Mountain; Itkillik River; Kavik River; Killik River; Kivalina River; Kongakut River; Lake Schraeder; Marsh Fork Canning River; Mount Fairplay; Mount McKinley National Park, Kanitshna; Murphy Dome; Noatak River Valley; Noluck Lake; Ogotoruk Creek; Sadlerochit Springs; Sagwon; Sheenjek River; Slime Creek and Nenana River; Toklat, Teklanika Rivers; Utukok River.

5.19 Erebia youngi

CANADA: North West Territories: Inuvic; Tununuk Point. Yukon Territory: Bear Creek Pass; Dempster Highway, mile 51, mile 82, mile 97; Firth River at Sheep Creek; Herschell Island; Kluane Lake; Nansen Creek; Old Crow; Siwash Creek.

UNITED STATES: Alaska: Aichilik River; Alaska Range; Anaktuvuk Pass; Big Lake; Eagle Summit; Galbraith Lake; Head of Canning River; Highway Pass; Hulahula River; Itigaknit Mountain; Kivalina River; Kongakut River; Lake Schraeder; Marsh Fork Canning River; McKarthey/Kennicott; Mount Distin; Mount Fairplay; Mount McKinley National Park; Mount McKinley National Park, Kantishna; Mountains between 40 mile and Mission Creeks; Nines Creek; Noatak River Valley; Noluck Lake; Nome and vicinity; Ogotoruk Creek; Sagwon; Sheenjek River; Steese Highway, mile 90.2; Toklat/Teklanika Rivers; Toolik Lake; Umiat, Gubik Gass Field; Utukok River.

5.20 Erebia dabanesis

UNITED STATES: Alaska; Kivalina River; Kongakut River; Lake Schraeder;

Noluck Lake; Nome and vicinity; Nome-Teller Road, mile 18, mile 21; Sheenjek River; Utukok River.

5.21 Erebia inuitica

UNITED STATES: Alaska: Anaktuvuk Pass.

5.22 Erebia callias

23 from Butterflies of the southern Rocky Mountains.

AUTOBIOGRAPHY

I was born on the 25th of December, 1954, in the city of Calgary, Alberta. Before I reached the age of two, my parents moved to Edmonton, Alberta, where I soon showed evidence of an interest in Entomology. Many an unfortunate coccinellid met an untimely end clutched a little too tightly in a grubby fist as my mother searched for an empty jar in which to house the remains of my catch.

My formal education began in Edmonton at the age of five. In 1967, my family moved back to Calgary, where I graduated from High School in 1971. By this time, my interest in insects was well established, and butterflies had become the focus of my attention.

After a collecting trip to the Yukon Territory in 1972, I entered the University of Alberta, in Edmonton, and completed a B. Sc. in Entomology in 1976. In my first year I met my future wife, Betty Avery, whom I married in 1975. In 1976 I became the father of a son, Nathan, who is already showing a strong interest in things living.

On completing the B.Sc., I entered a M.Sc. program under the supervision of Dr. G. Ball, the results of which are reported herein. My support during the period of research was through research and teaching assistantships.